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THE WOODS HOLE OCEANOGRAPHIC INSTITUTION
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Contribution No. 340

Vol. X, Art. 4.

STUDIES ON THE MORPHOLOGY AND SYSTEMATICS OF THE FAMILY HALARACHNIDAE OUDEMANS 1906 (ACARI, PARASITOIDEA)[1]

BY IRWIN M. NEWELL[2]
Woods Hole Oceanographic Institution
Woods Hole, Massachusetts

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ABSTRACT

In this study the present status of the systematics of the Halarachnidae parasitic in Pinnipedia is summarized, the major deficiencies are indicated, and the points which must receive critical attention in the future are outlined. A number of misconceptions regarding certain structures, most notably the chelicerae, legs, tracheae and endosternite, are clarified and post-larval development is discussed. The existence of two natural species groups is demonstrated and the new genus *Orthohalarachne* is created for *Halarachne attenuata* Banks and its congeners. *Halarachne americana* Banks, *Orthohalarachne diminuata* (Doetschman) and *O. attenuata* (Banks) are redescribed and figured in detail. All other species are listed, and references, hosts and ranges are given. *Pneumonyssus* Banks is covered very briefly to complete the treatment of the family.

[1] Contribution No. 340 of the Woods Hole Oceanographic Institution.

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INTRODUCTION

The principal objectives of this study are to consolidate our present knowledge of the systematics of the Halarachnidae parasitic in Pinnipedia, to indicate the major deficiencies, and to outline the points which must receive critical attention in the future development of the systematics of the family. Indeed, certain of the ideas set forth here will be found generally applicable to the solution of the peculiar morphological, systematic and biological problems presented by that heterogeneous group of Parasitoidea which inhabit the respiratory tracts of higher vertebrates.

Previously, all parasitic mites taken from the respiratory passages of Pinnipedia have been referred to the genus *Halarachne* Allman 1847, but detailed study of the morphology of these mites shows that there are two well defined and natural groups of species which differ consistently and in so many characters that they must be considered generically distinct. Accordingly, the new genus *Orthohalarachne* is created herein for those species congeneric with the type, *Halarachne attenuata* Banks 1910, which was the first described species of this group.

The references given for each species are not necessarily complete, but all papers having an important bearing on systematics and morphology are listed. All figures were drawn by the author with the aid of a camera lucida. Scales are given for most drawings and these can be used with reasonable confidence in obtaining measurements not given in the text. The scale for Figs. 1, 3, 10 and 28–31 represent 500μ, each division representing 100μ. In all other cases each subdivision of the scale represents only 10μ, so that a scale with three subdivisions equals 30μ, one with ten subdivisions is 100μ, *etc.* In all 100μ scales a longer mark has been made at the 50μ point.

Unfortunately the many gaps in our knowledge of the anatomy of certain of the species makes it impossible to provide a reliable key, but there are few species in the family, so that there is no particular necessity for a key at this time. Thus, there are at present four species of *Halarachne*, six of *Orthohalarachne* and seven of *Pneumonyssus*, a total of 17 species for the family.

FAMILY HALARACHNIDAE OUDEMANS 1906

Diagnosis. Dorsal plate of both male and female undivided, characteristically marked by insertions of muscles on inner surface (Fig. 18), finely and densely punctate. Tritosternum absent (see discussion under *Orthohalarachne diminuata*, p. 260). Sternal plate longer than broad; only 3 pairs of sternal setae present; metasternal setae absent. Jugularia absent. Genital opening of male at anterior margin of sternal shield. Genital opening of female a simple transverse slit between coxae IV. Rudimentary genital plate behind female genital opening; setae lacking in genital area. Coxae I–IV respectively with 2, 2, 2 and 1 setae ventrally. Three anal setae present as a rule, but sometimes 4 (the dorsal seta duplicated). Chelicerae 3-segmented. Digitus fixus of chelicera sometimes greatly reduced, shorter than digitus mobilis (Figs. 7, 38, 55, 60). Spermatophore bearer absent from male chelicera. A minute seta dorsally at base of digitus fixus. Epistome simple, triangular. Hypostome triangular and pilose. Maxillary palpi of adult with 4 segments, the tarsus and tibia fused. Tarsal prong bifid. Stigma lying above interval between coxae III and IV, or above IV, or even slightly behind IV. Peritreme very short, reaching only to level of posterior margin of coxa III, if that far. Peritremalia (Fig. 35) reaching to level of anterior margin of dorsal plate, but interrupted over coxa III. Tracheal system extensively developed, the stigmata of opposite sides joined by a transverse trachea.

Type Genus. Halarachne Allman 1847.

Remarks. Whether the above diagnosis is broad enough to include *Pneumonyssus* Banks 1901 cannot be stated, for the morphology of that genus has not been worked out completely, but the writer feels that it should be retained in the *Halarachnidae* for the present.

Morphological Observations. The following critical account of certain morphological aspects is presented in the hope that others will use it as a guide in clarifying the morphology of related genera, since it is only by such very detailed study that we can hope to arrive at a natural classification of the Parasitoidea. In the discussion the above diagnosis has been used as an outline. It should be remembered that the discussion applies primarily to *Halarachne* and *Orthohalarachne*, the only genera of the family of which the writer has firsthand knowledge. The extreme importance of technique has been pointed out, since many of the questions that still remain in the taxonomy and morphology of the group have their origin in improper or inadequate technique.

Sternal and genital plates. The outline of the sternal plate is difficult to determine except in properly prepared specimens, and yet it is of utmost importance that this plate be accurately delimited, especially with regard to its relationship to the sternal setae. There are numerous open questions in the taxonomy of the family which are due entirely to the failure of workers to clearly point out the extent of the sternal plate and the position of the sternal setae. For example, Ferris (1942: 79–80) was uncertain whether or not his *Halarachne miroungae* was identical with, or distinct from, *H. halichoeri*. His two published figures (1925: 163–167; 1942: 79–80) of the species omit the third sternal seta, the position of which is a critical character for distinguishing between *H. halichoeri* and *H. americana* (see p. 244). Doetschman (1944: 68–72) showed the female of *Orthohalarachne diminuata* (Doetschman) as having all three sternal setae outside the sternal plate, and yet it is clear from his description (p. 70) that he had difficulty in finding the outline of the sternal plate in the male. All this leaves considerable uncertainty about the accuracy of the description. This is unfortunate, for although there is no doubt that the forms described in the present paper (in which the sternal plate includes three pairs of setae) are *O. diminuata*, the highly interesting possibility of demonstrating subspeciation must be set aside because it is not certain that the sternal setae of Doetschman's specimens were really outside the plate.

The extent of the sternal and genital plates can be definitely established only by careful study of properly mounted specimens at high magnifications after the soft parts have been removed by a noncaustic hydrolytic agent (*e. g.*, trypsin) and the specimens then mounted in a medium of low or high refractive index (*e. g.*, glycerine or Hyrax, but not balsam or Clarite) for study at magnifications of 1000–1600. Staining is not only unnecessary but may result in erroneous observations. The extent of the lightly pigmented portion of the plates is deceptive, for the very margin of the plate is usually as colorless as the membranous area and can be seen only as a *change in texture of the cuticle*. In this connection it is important to note that it is impossible to properly treat material which has been in formalin, since the soft parts cannot be hydrolyzed; therefore, only alcohol should be used as a preservative.

The use of the genital shield of the female as a critical specific character (Finnegan, 1934: 326) is of questionable value, since the structure is weakly developed and highly variable in form and size, at least in *Orthohalarachne attenuata* (Figs. 43–53).

Chelicerae. There is considerable confusion with regard to the morphology of the male chelicera of *Orthohalarachne*, although the female chelicera is relatively simple and was correctly understood by Oudemans (1926d). In the female the tarsus (= digitus mobilis) forms the main distal portion of the chelicera (Figs. 38, 60) and bears an elaborate membrane on the dorsal surface. The digitus fixus, although reduced and modified, can be identified by its position and by the presence of the dorsal seta at its base. This seta is found in numerous genera of predaceous Parasitoidea in which the chelicerae are of more normal form, and in these genera the relation of the seta to the digitus fixus is the same as in *Orthohalarachne.* It should be noticed that the relative hypertrophy of the tarsus, as contrasted with the atrophy of the digitus fixus, has resulted in a ventral and medial displacement of the latter. The digitus fixus is bifid distally.

Turning to the male we find a similar situation (Fig. 36). There is a large tarsus which is identified by the apodemes of the levator and depressor muscles, and at the base of the tarsus is a structure which is similar to the digitus fixus of the female (compare Fig. 36 with 38). The base of this structure is somewhat more medially displaced than in the female, but the entire chelicera is hypertrophied as compared with that of the female, and this displacement is quite certainly associated with the hypertrophy. The distal portion of the structure is bifid, as is the digitus fixus of the female. Oudemans (1926d: 94, 105) considered that this two-pronged process in the male was the spermatophore bearer, with the digitus fixus represented by a small protuberance (Oudemans: fig. 88, *fi*). Oudemans misinterpreted this protuberance, for the closest study by the present writer reveals that it is only the point where the tarsus articulates dorsally with the basal portion of the chelicera. The + in Fig. 36 shows this swelling, in front of which is the articular membrane, each indicated by an arrow. Even overlooking the morphological evidence, it seems unlikely that such a highly adaptive structure as the spermatophore bearer would persist while the relatively conservative digitus fixus dropped out. Oudemans himself considered the "spermatophore bearer" (*i. e.*, digitus fixus) nonfunctional (p. 94, "Offenbar hat der wirklich Digitus mobilis die Funktion, die Spermatophore überzutragen, übernommen"). Of course, nothing is known of sperm transfer in the Halarachnidae, but Oudeman's surmise could very well be correct.

In summary, the present writer finds it impossible to accept Oudemans' interpretation of the structure of the male chelicera in *Orthohalarachne.* The "Spermatophorenträger" of Oudemans is the digitus fixus, while his "digitus fixus" is just a local thickening in the wall of the chelicera at the dorsal articulation of the digitus mobilis. A spermatophore bearer is completely lacking. Both males and females of *Halarachne* also have a digitus fixus (Oudemans 1926d: 82; figs. 17, 28); and the male lacks a spermatophore bearer. Although the chelicera of the female is normally oriented throughout, the distal portion of the chelicera of the male is rotated somewhat, and the hook-like tarsi oppose each other medially (see Oudemans 1926d: fig. 54). Dissected chelicerae compressed between coverslips are apparently twisted, because the basal portion is higher than wide, whereas the tarsus is wider than high. This torsion, while it results in an unnatural condition for *Orthohalarachne*, restores the primitive morphological relationship between the tarsus and the rest of the chelicera. This fact must be remembered while studying the figures of the male chelicerae in this paper.

The structure of the chelicera of *Pneumonyssus* Banks 1901 is still an open question, as it has not yet been accurately described or figured. Vitzthum (1931g: 59) stated of *P. simicola* Banks 1901, "Vom Digitus mobilis ist nichts erhalten als der ihm primär aussen seitlich angefügte Spermatophorenträger," which is interpreted by the writer as "Nothing remains of the digitus mobilis but the . . . spermatophore bearer." Although the present writer has not had the opportunity to study *Pneumonyssus*, he suspects that Vitzthum's interpretation of the structure of the chelicera was morphologically incorrect, for when accurate study is made it will probably be found that there is *no spermatophore bearer whatever.* Finally, the "hakenförmige Spermatophorenträger" of *Pneumonyssus duttoni* Newstead (see Oudemans 1935b: 502–503) is beyond all doubt the digitus mobilis and not the spermatophore bearer. Even if the digitus mobilis takes over the function and shape of a spermatophore bearer, it still remains the digitus mobilis, to which are attached the apodemes of the levator and depressor muscles!

Palpi. It is clear from the position of the tarsal prong in most Halarachnidae that tibia and tarsus have been fused, forming a tibiotarsus. Thus, in Parasitoidea with five-segmented palpi, the prong lies at the extreme proximal end of the short tarsus, whereas in *Ortho-*

halarachne and *Halarachne* it lies at the middle of the terminal segment, which is relatively very long (nearly twice as long as the preceding segment).

Legs. Doetschman (1944: 70) stated of the larva of *Orthohalarachne diminuata*, "The distal segments have false articulations plainly visible dorsally on legs II and III; this fusion results in a tibiotarsus." The latter part of the statement is incorrect, for a tibiotarsus is derived by the fusion of the tibia and tarsus (as in the palpi of *Halarachne* and *Orthohalarachne*). However, there is no suggestion of fusion of the tibia and tarsus in the legs. The tarsus is incompletely divided into two parts, the basal one of which is the basitarsus, the distal one the distitarsus.

Tracheae. In his original description of *Halarachne halichoeri*, Allman (1847: 49) stated, "One great transverse trunk (fig. 2g) passes across the posterior part of the cephalothorax, uniting the tracheary systems of opposite sides." But Oudemans (1926d: 54–55) disagreed with this, saying "Er muss etwas anderes für eine Trachee gehalten haben; vielleicht den vorderen Rand der nach vorn konvexen unteren Genitallipen, wenn man diesen Ausdruck gebrauchen darf." Allman was correct in his observation, for the present writer has found a transverse tracheal trunk in *Halarachne americana*, *Orthohalarachne attenuata* and *O. diminuata* (Fig. 54, shown by double row of dotted lines between the stigmata). Steding (1923: 453) also said that such a "Queranastamose" existed in *O. zalophi* (= *Halarachne otariae* Steding 1923), and was shown in her plate III, fig. 17, *Tr.* Reference to this figure shows no *Tr.*, but an error obviously had been made here. The "Dorsaldrüse" was labelled in fig. 16, but in fig. 17 "Ddr" indicated a structure which is thin-walled, oval in cross-section, and lies under the posterior end of the dorsal gland. This was undoubtedly meant to be *Tr*, since it is in the position occupied by the transverse trachea in *O. attenuata.*

In a dissection of *O. attenuata* a section of trachea was found which had been partly unwound, revealing its spiral structure (Fig. 21). This demonstrated that the tracheae of at least some Acari are essentially identical with those of insects in regard to the ctenidia. The spiral chitinous thread is continuous for considerable lengths.

The stigma lies in a small circular plate (the stigmal plate) from which extends the short peritreme. The stigma and peritreme are usually surrounded by a faintly outlined plate, the peritremalia, which extends from the level of coxa I to behind coxa IV, but is interrupted over coxa III. In *O. diminuata* the posterior portion of the peritremalia is very weakly developed.

Genus *Halarachne* Allman 1847

Diagnosis. Opisthosoma of gravid female saccate, not clavate (in forms known at present). Male and female with more than 4 pairs of setae dorsally between posterior margin of dorsal plate and anal plate; also ventrally, between level of coxae IV and anal plate. Digitus mobilis of chelicera of male tubular, sinuate in form, not forming a discrete hook; bearing a small dorsal lamella which is scarcely as broad as the tubular portion of digitus mobilis at same level (Oudemans 1926d: figs. 27–28). Maxillary palpi 4-segmented, the tarsus and tibia fused. Tarsal prong bifid. Adults with 4 pairs of maxillary setae ventrally (Fig. 5), including 2 pairs of small setae at tips of malae exteriores. Ventral surface of mala exterior without rudimentary seta. Larva and female (also male?) with 2 pairs of setae medially on P-2 (a total of 5 are found on the segment). Larva with dorsal anal seta longer than lateral anal setae; only 2 pairs of ventral maxillary setae present (those at tips of malae exteriores).

Distribution. North Atlantic Ocean; Pacific Coast of North America; South Orkneys (?); probably as widely distributed as the Pinnipedia, or at least the Phocidae.

Type. *Halarachne halichoeri* Allman 1847.

Synonyms. *Rhinixodes* Nehring 1884 and *Rhinacarus* Nehring 1884. Both were proposed as possible substitutes for *Halarachne* on the grounds that they were more appropriate.

Hosts. It is significant that there are no host records for *Halarachne* species outside of the family Phocidae. Oudemans (1926d: 108) stated "Ich habe mich davon überzeugen können, dass *Phoca vitulina* keine *Halarachne* birgt." We know today, of course, that *Phoca vitulina* does harbor *Halarachne*, at least in western North America.

1. *Halarachne halichoeri* Allman 1847 (but not of Ferris)

Thompson 1844, 291: *Halarachne halichaeri* Allman (nomen nudum). Allman 1847, 47–51: *Halarachne halichoeri.* Murray 1876, xi, 167–169: *Halarachne halichaeri* (Allm. 1847). Nehring 1884, 58–64: *Halarachne Halichoeri* Allman 1844. Steding 1923, 443, 448, 458, 474, 475, 488–490: *Halarachne Halichoeri* Allm. Ferris 1925, 163, 166: *Halarachne halichoeri* Allman. Oudemans 1926d, 49–86, 88, 90, 96, 99, 107: *Halarachne halichoeri* Allman 1847. Vitzthum 1929a, 4, 28: *Halarachne halichoeri* (Allman). Viets 1927b, 70–71: *Halarachne halichoeri* Allman. Finnegan 1934, 326: *Halarachne halichoeri.* Oudemans 1935b, 470: *Halarachne halichoeri* Allman 1847. Ferris 1942, 77–79: *Halarachne halichoeri* Allman 1847 (also misspelled *Halirachne*).

Distribution. Ireland to Baltic Sea.

Host. *Halichoerus grypus* (Fabricius), (Pinnipedia, Phocidae).

Remarks. Ferris has recorded this species from the Pacific coast of North America, but it is not clear from his work that this is correct. He compares Pacific specimens with *Orthohalarachne zalophi* (= *Halarachne zalophi*) and with *Halarachne miroungae* Ferris 1923. As is shown here, the former species is not even in the same genus, and Ferris' comparison of *H. miroungae* with *H. halichoeri* (?) is based on purely relative characters in which variations may be due either to individual differences or to age. Therefore, the existence of *H. halichoeri* on the Pacific coast has not been substantiated. The present writer prefers to refer all Pacific coast records to *H. miroungae* until more critical study shows that they should be treated otherwise. This problem is discussed further under *H. miroungae.* Ferris himself questions the specific identity of *H. miroungae;* hence he must question the validity of the characters upon which he based his comparison of *H. halichoeri* Allman, Ferris with *H. miroungae* Ferris.

2. *Halarachne miroungae* Ferris 1925

Ferris 1925, 164–167: *Halarachne miroungae* n. sp. Doetschman 1941, 23: *Halarachne miroungae* Ferris. Ferris 1942, 78–80: *Halarachne miroungae* Ferris 1925. ? Scheffer *et* Slipp 1944, 400: *Halarachne halichoeri.*

Distribution and Hosts. *Mirounga angustirostris* (Gill), (Phocidae): Guadalupe Island, off Baja California (ca. 29° N., 118° W.);

Phoca vitulina richardii (Gray), (= *Phoca richardii*): California (Pacific Grove, ca. 36° 28′ N., 122° W.); Washington (Nisqually, ca. 47° 15′ N., 122° 30′ W.). The Washington record is for *H. halichoeri* Allman, Ferris.

Remarks. The complexity of the situation in the Pacific *Halarachne* species is indicated in the following possibilities.

1. There is a single species, a) *H. miroungae,* or b) *H. halichoeri.*

2. There are two species, a) *H. miroungae* and an unnamed species, b) *H. miroungae* and *H. americana,* c) *H. miroungae* and *H. halichoeri.*

Of these, 1a or 2a is considered by the present writer to be most likely, with 1b and 2c highly improbable. There is at least one morphological clue which can be drawn from Ferris' work. Ferris (1925: fig. 1A; 1942: fig. 37b) showed the posterior end of the sternal plate reaching scarcely beyond the level of the posterior margin of coxa III, just as in *H. americana.* Oudemans (1926d: fig. 14) showed it reaching beyond the level of the anterior margin of coxa IV in *H. halichoeri.* This would indicate that the sternum of *H. miroungae* is smaller than the sternum of *H. halichoeri,* that the third pair of sternal setae lie outside the plate, and that therefore *H. miroungae* and *H. halichoeri* are distinct. However, in the form of the peritreme and the chelicerae, *H. miroungae* is closer to *H. halichoeri* than to *H. americana.*

3. *Halarachne americana* Banks 1899[3]

Banks 1899a, 212–214: *Halarachne americana* n. sp. Ferris 1925, 163, 166: *Halarachne americana* Banks. Oudemans 1926d, 49, 83–85: *Halarachne americana* Banks 1899. Finnegan 1934, 326: *Halarachne americana* Banks 1899. Ferris 1942, 78: *Halarachne americana* Banks. Doetschman 1944, 71: *Halarachne americana* Banks 1899.

Distribution and Host. Monachus tropicalis Gray (Phocidae). The type was collected from a zoo specimen. Finnegan (1934: 326) pointed out, " . . . it is doubtful whether one is justified in regarding the distribution of the host (West Indies, Coast of Yucatan to Florida and Bahamas) as established for the parasite." However, the fact that the species is distinct from both *H. halichoeri* and *H. miroungae* increases the probability that the host record is not misleading in this case, and that the distribution of *H. americana* is the same as for *Monachus tropicalis.*

The generic and family characters have been given in detail above and are not repeated in the following description of the species.

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[3] Through the kindness of Jos. Bequaert and Nathan Banks of the Museum of Comparative Zoology, the writer has obtained cotypes of *Halarachne americana* upon which this redescription is based. The specimens apparently had been mounted directly in balsam, for the surface of the body was covered with minute droplets of water. Although over 45 years old, the mites responded well to trypsin hydrolysis and were remounted in glycerine.

Female. The three females had the following dimensions (body length is dorsal length to base of capitulum):

	1	2	3
Body length	2866μ	2855	1855
Max. width, podosoma	1113	1113	tilted
Max. width, opisthosoma	1425	1450	tilted
Length, dorsal plate	1360	1427	1394
Max. width, dorsal plate	697	674	686
Ratio of L/W, dorsal plate	1.95	2.12	2.02

The third female (Fig. 1) is an adult but not yet completely mature. Fig. 3 shows the normal form of the distended female. The posterior portion of the dorsal plate, behind the level of maximum width, is relatively longer than in *H. halichoeri*. Only 3 pairs of setae are large enough to be seen, but dissections would probably reveal others.

Anal plate tending to be disti-dorsal in the gravid females but completely terminal in the nongravid female. Tritosternum absent. Sternal plate with only 2 pairs of setae, the third pair lying far outside the plate and more widely separated than the second pair in distended females (but not in the undistended female). The sternal plates of the three females measured 427 x 281, 416 x 280, and 450 x 292 μ (L/W = 1.52–1.54). Post-coxal apodemes approaching sternal plate, but not reaching it, and not forming pigmented horn-like processes of the plate. They are apparent only because of their refractility. Sternal plate not reaching beyond level of posterior margin of coxa III.

Ferris (1942: 78) said "An immediately noticeable feature of *halichoeri* is the appearance of the so-called 'endosternite' which is an internal sclerotization arising from the sternal plate between the coxae . . . forms four pigmented points." Ferris was referring not to the endosternite but to pigmented portions of the sternal plate. The endosternite in the Halarachnidae, as in all Arachnida, is an internal sclerite which has no connection with the sternal plate. Also, the writer knows of no Acari in which the endosternite is pigmented.

In *Halarachne americana* post-coxal apodeme III is so weakly developed that it could be mistaken for a fold in the cuticle. That behind IV is continuous with the peritremalia laterally and extends to the margins of the genital opening, where it joins with (or is produced into) a heavy spur-shaped apodeme, oriented longitudinally. Post-coxal apodeme IV lightly pigmented in the older female but simply refractile in the younger one. However, in all three the spur-like apodeme is reddish-brown.

In Fig. 10 the genital opening is gaping. The line just posterior to the sternal plate is the anterior margin; the other line is the posterior margin. The space between is the dorsal wall of the vagina. Genital plate variable in size and form. A median row of 6 to 7 pairs of setae between genital plate and anal plate, easily seen in young female but difficult to discern in older ones; some of them covered by secretions of the cuticular pores. Also, the opisthosoma is so greatly enlarged that the setae are relatively insignificant. Oudemans found a row of 6 pairs of setae in this position in the male of *H. halichoeri* but none in the female. Since young females of *H. americana* (in which the abdomen has the same form[4] as that of the males of both *H. halichoeri* and *H. americana*) have these 6 pairs of setae, just as in the male of *H. halichoeri*, the chaetotaxy of the opisthosoma is apparently identical in both sexes and in both species. Oudemans probably did not find the setae in the female of *H. halichoeri* because he had old distended specimens and not because the setae were absent.

The ventral cuticle of the opisthosoma is pierced by many cuticular pores (Fig. 14) which are found also on the dorsal surface as well as sparsely distributed over the podosoma. In young females nearly all these pores are clean; their walls are refractile and project slightly beyond the surface of the cuticle. In older females many of the pores are surrounded by irregular patches of a light brown secretion, especially abundant anterior and posterior to the stigmata at the sides of the body (Fig. 3). Here the secretions of adjacent pores sometimes coalesce to form small, irregular patches. In the two females seen,

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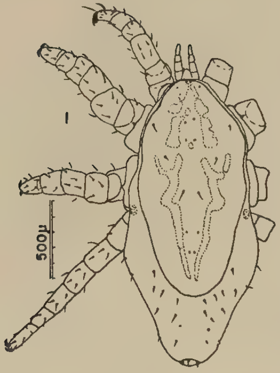
[4] Banks (1899a); also quoted by Oudemans (1926d: 84). "The male . . . is smaller than the female and the abdomen does not extend much beyond the dorsal shield, and is much narrower behind; . . ."

Figures 1–14. *Halarachne americana* Banks 1899. *1* Female: dorsum of young, undistended individual (scale = 500μ). *2* Female: palp, median view. *3* Female: dorsum of older, distended individual (scale = 500μ). *4* Female: left tarsus I, dorsal view. *5* Female: capitulum, ventral view (inclined distiventrally at angle of 18°). *6* Female: chelicera, lateral view. *7* Female: chelicera of young female, median view of distal portion. *8* Female: chelicera of older female, lateral view of distal portion. *9* Female: palpal tibiotarsus, median view of distal portion. *10* Female: podosoma of older individual (scale = 500μ). *11* Female: palpal tibiotarsus, lateral view. *12* Larva: posterior end of opisthosoma, ventral view. *13* Female: posterior end of sternal plate; genital opening; ventral view, young female. *14* Female: ventral surface of opisthosoma of undistended individual, about halfway between genital opening and anus.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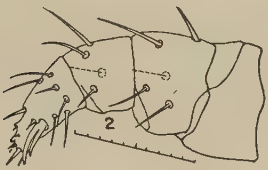
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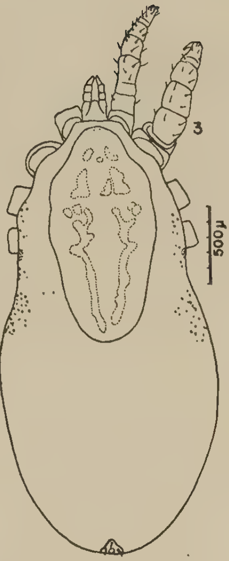
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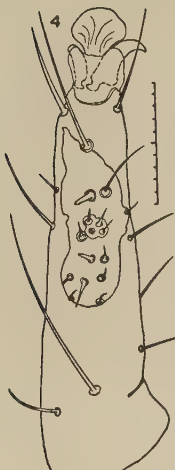
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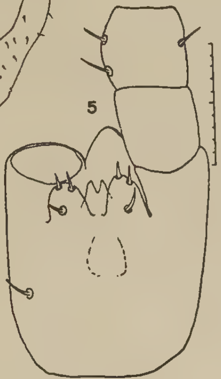
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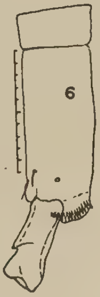
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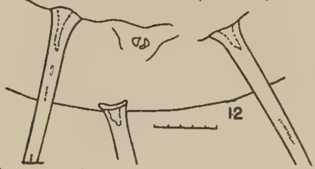
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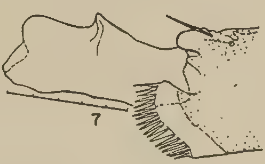
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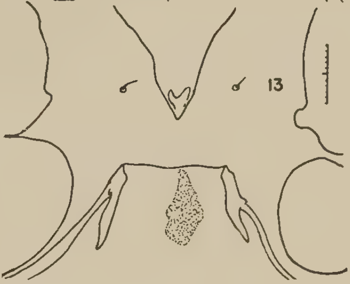
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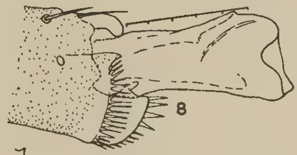
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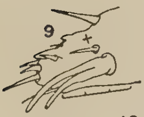
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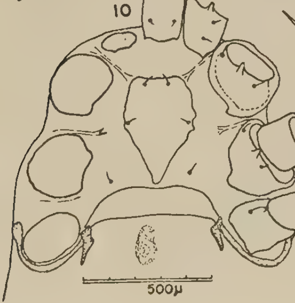
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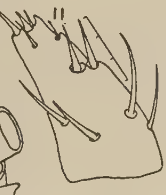
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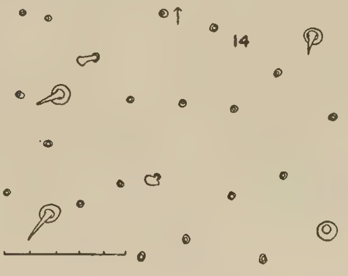
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however, there is nothing approaching the condition in older females of *H. attenuata* where large portions of the body in the region of the dorsal plate are sometimes covered with grotesque, scab-like patches.

Peritremalia (Fig. 15) interrupted over coxa III. Stigmal plate not sharply delimited from peritreme. The latter crescentic in form, convex posteriorly. Stigma and peritreme within a deeply pigmented circular plate which is convex (seen from above). The peritreme in *H. halichoeri* is markedly different (compare with Oudemans 1926d: 73, 74).

Digitus fixus of chelicerae (Figs. 6, 7, 8) apparently even more reduced than in *H. halichoeri*, bearing a dorsal setiform projection which does not appear to be a true seta since it lacks a typical alveolus. The dorsal spiniform process on the tarsus can be identified with a similar process in *H. halichoeri* (see Oudemans 1926d: figs. 16–18). The portion of the tarsus beyond this process drops off sharply in *H. halichoeri* and bears a number of sharp teeth, but in *H. americana* the distal portion of the tarsus is as high as the basal portion and is not dentate in the two specimens dissected by the writer. One of these (Fig. 7) is the young female, the other is one of the older females (Fig. 8).

Ventral surface of capitulum as shown in Fig. 5. In the specimen drawn, one of the posterior maxillary setae is lacking. Palpi as shown in Figs. 2, 9 and 11. The + above the tarsal prong in Fig. 9 shows where an additional seta is found in one of the other palpi. Two spine-like projections of the dorsal surface of the tarsus present as shown, 3 setae terminally, the ventral one long, the dorsal ones short.

Male. Not seen by the writer.

Larva. Four larvae measured from 1439 to 1607μ in length. No characters of specific value were noted. The chaetotaxy of the body is as shown by Oudemans (1926d: figs. 1–2, *H. halichoeri*) with one slight and probably variable difference. Oudemans showed a postero-lateral pair of setae on both dorsal and ventral surfaces. In the larvae of *H. americana* both pairs are dorsal, but the most posterior of these (homologous with the ventral pair shown by Oudemans) is almost completely lateral. Anal setae with very heavy hyaline shafts, completely solid for much of their length, or containing at most a minute medulla which is frequently interrupted (Fig. 12), (the anal setae of *Orthohalarachne* are thin walled and hollow except in the distal 10 or 15% of their length).

4. *Halarachne* sp. Blanchard 1906

Blanchard 1906, 313: *Halarachne* sp. Steding 1923, 443: "Milben aus den Nasenhöhlen von *Leptonychotes leopardinus*, R. Blanchard." R. Blanchard is not to be taken as the author of *L. leopardinus*.

Distribution. South Orkney Islands (Orcades du Sud), (ca. 61° S., 46° W.).

Host. Leptonychotes weddelli Allen (= *L. leopardinus*). "Weddell Seal." (Phocidae, Cystophorinae).

Remarks. This species was not described by Blanchard (1906: 313) because he believed he had only larvae and "nymphs" ("Les larves hexapodes et les nymphes octopodes ont la plus grande resemblance avec celles de l'*Halarachne halichoeri* . . . Toutefois en l'absence des adultes; . . ."). Since there is no nymphal instar in the Halarachnidae, Blanchard's "nymphes octopodes" obviously were adults. It is not even certain that this species is a *Halarachne*, for nonattenuate specimens of *Orthohalarachne* could be mistaken for *Halarachne* if not examined closely. However, the fact that it was taken from a host of the family Phocidae is an indication that it belongs in *Halarachne*, for no species of *Orthohalarachne* has yet been reported authentically from the Phocidae. If this is a true *Halarachne* it is the only record of the genus (in the sense used in this paper) from the southern hemisphere.

Genus *Orthohalarachne*, new genus

Diagnosis. Opisthosoma of gravid female clavate in most forms; saccate in *Orthohalarachne diminuata.* Male and female with 2 pairs of setae dorsally between posterior margin of dorsal plate and anal plate, and also ventrally between level of coxae IV and anal plate. Digitus mobilis of chelicera of male forming a heavy hook and bearing a large foliaceous lamella which at its broadest level is twice as broad as the hook at the same level. Digitus fixus often bifid. Adults with only 2 pairs of long maxillary setae ventrally (Fig. 39) and a pair of rudimentary setiform structures ventrally on the malae exteriores (Fig. 20). Larva, male and female with only 1 pair of setae medially on P-2 (a total of 4 for the segment in the adult, and 3 in the larva). Larva with dorsal anal seta very short, much shorter than lateral anal setae, and often duplicated; no ventral maxillary setae present.

Distribution. North Atlantic Ocean, Pacific coast of North America, Falkland Islands.

Type. *Orthohalarachne attenuata* (Banks) 1910 (= *Halarachne attenuata* Banks 1910).

Hosts. Whereas *Halarachne* species have thus far been reported only from hosts of the family Phocidae, *Orthohalarachne* species are known only from hosts in the other two families of Pinnipedia, *viz.*, the Otariidae and Odobenidae.

1. *Orthohalarachne attenuata* (Banks) 1910[5]

Banks 1910a, 3, 12: *Halarachne attenuata*, new species. Oudemans 1926d, 50, 85: *Halarachne attenuata* Banks 1910. Finnegan 1934, 326: *Halarachne attenuata* Banks 1910. Ferris 1942, 78: *Halarachne attenuata* Banks 1910.

Distribution. Pribilof Islands in Bering Sea (57° 5′ N., 170° 25′ W.) to Depoe Bay, Oregon (44° 50′ N., 124° 5′ W.).

Hosts. *Callorhinus ursinus cynocephalus* (Walbaum), (Bering Sea and Oregon); *Eumetopias jubata* (Schreber), (Bering Sea), (Otariidae).

Type locality and host. The type data were given simply as (Banks, 1910a: 3) "Taken from a seal pup at St. Paul Island, by Mr. J. Judge, October 7, 1909." Oudemans (1926d: 85) incorrectly concluded that this is the St. Paul Island in the southern Indian Ocean (48° 35′ S., 77° 40′ E.), while Finnegan (1934: 326) assumed that this is the St. Paul Island of the Bering Sea, which is correct. Ferris (1942: 78) stated: "The host was in all probability the fur seal, *Callorhinus alascanus*, although it could have been a species of the genus *Phoca*, or of *Erignathus*." The latter two possibilities undoubtedly need not be

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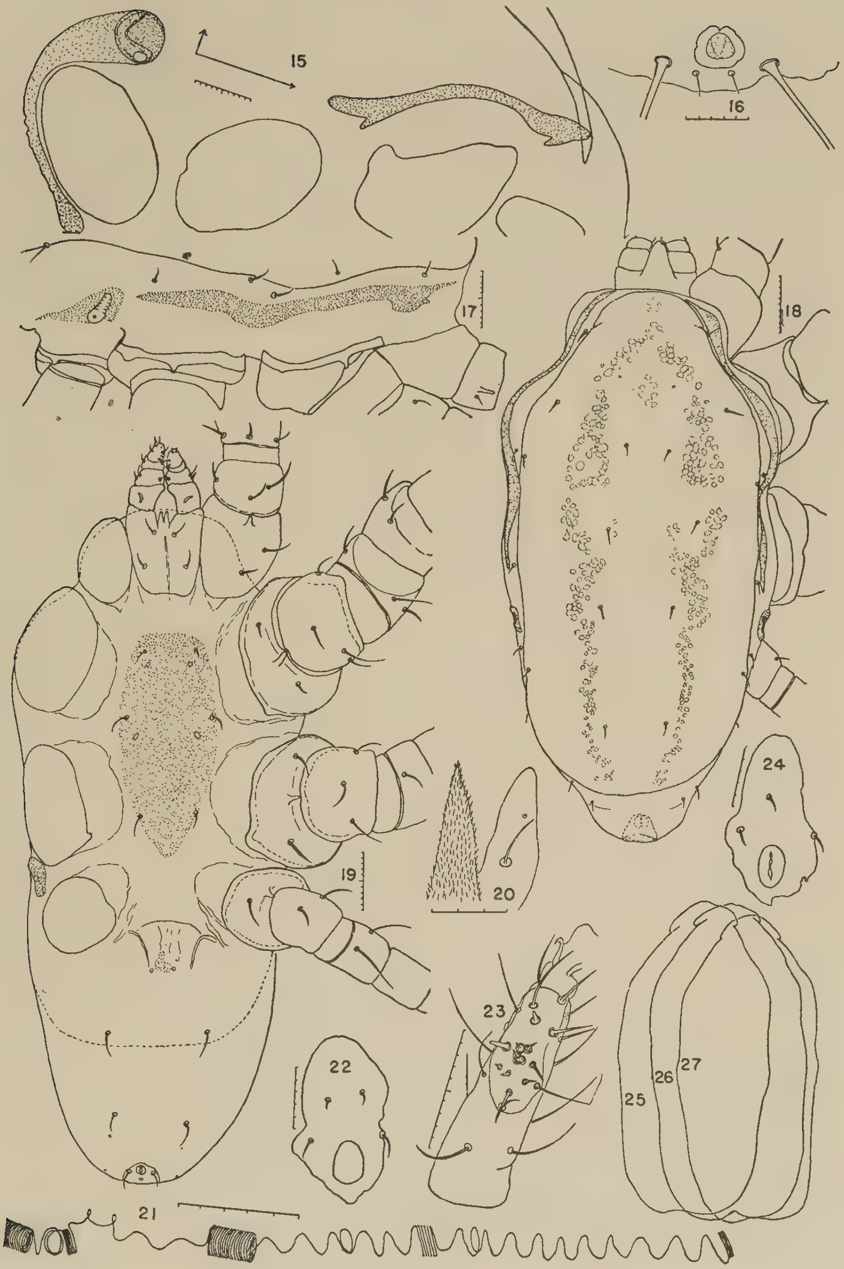
[5] V. B. Scheffer of the United States Fish and Wildlife Service collected the parasitic mites of seals on St. Paul Island on which are based the present morphological and systematic findings regarding the new genus *Orthohalarachne*. He has also provided the writer with the material from Depoe Bay, Oregon. The United States National Museum loaned the writer specimens of *Orthohalarachne attenuata* (Banks) 1910, taken from *Callorhinus ursinus* on "St. Paul Island, Alaska, from posterior nares of fur seal pup, 10 Sept. 1910" (data on slide).

Figure 15. *Halarachne americana* (continued). Female: podosoma, lateral view showing peritremalia, stigma, peritreme, *etc.*

Figures 16–27. *Orthohalarachne attenuata* (Banks) 1910. *16* Larva: anal region, ventral view. *17* Female (young, nonattenuate specimen): podosoma, dorso-lateral view. *18* Male: dorsum. *19* Female: venter. *20* Male: hypostome and mala exterior, ventral view. *21* Adult: trachea of dissected specimen. *22* Male: anal plate, posterior view. *23* Female (from *E. jubata*): tarsus I, dorsal view. *24* Male: anal plate, posterior view. *25* Female (from *C. ursinus;* St. Paul): dorsal plate. *26* Female (from *C. ursinus;* Oregon): dorsal plate. *27* Female (from *E. jubata;* St. Paul): dorsal plate.



considered. V. B. Scheffer stated (by letter) that "The seal pup from which the type of *attenuata* was collected was without question a first-summer fur seal. When seal is referred to on the islands, the name has only one meaning. The collector, James Judge, was for many years an agent in charge of sealing operations." This should remove all uncertainty as to the type locality and type host.

This species is redescribed from over thirty of several hundred specimens from the type locality and type host. V. B. Scheffer's collection also contains material of considerable interest in the life history of the Halarachnidae. The generic and family characters are not included, since they have been given in detail above.

Female. Body 930–4500μ long (Figs. 28–31), depending on age. Dorsal plate 899–978μ long, 427–472μ wide (L/W = 2.00 to 2.28), based on 10 females. Vertex setae absent. Other setae, panelling and pores as shown in Fig. 18. Anal plate (Figs. 22, 24) completely terminal as a rule; dorsal anal seta often duplicated as in larva. In one specimen there are 3 dorsal anal setae (in addition to the lateral setae) and a vestigial setal alveolus.

In the original figure the dorsal plate is represented by Banks as having a knob-like process at the anterior end and a deep notch at the posterior end. Both of these features are somewhat exaggerated in the drawing and variable in nature. In most specimens there is only a suggestion of a constriction at the anterior end under low power, but under high power it is seen that this is due principally to lighter pigmentation where these notches appear. The feature is more apparent in old individuals than in young ones. A posterior concavity is often present, but in no specimen has it been found as marked as in the original figures, and it may be completely absent. In the latter case the posterior margin of the plate is straight or slightly convex.

Tritosternum absent. In certain older specimens an indistinct, irregular patch of moderately refractile cuticle appears in the region between the anterior margin of the sternal plate and the capitulum, or there is sometimes a small fold here. It must be remembered that this area is subject to considerable flexion; local cuticular thickenings and folds are common in such regions. Also, numerous Parasitoidea with a tritosternum have other small sclerites developed in this region. There seems to be no logic in assuming, as some writers have, that a refractile area in this position must be a rudimentary tritosternum. The author prefers to consider that a tritosternum is completely lacking, since it has never been demonstrated that one exists in any of the *Halarachnidae.* Sternal plate including all 3 pairs of sternal setae and 2 pairs of pores. Post-coxal apodemes I, II and III very weak or absent; those behind IV continuous with the posterior portions of the peritremalia, in which are enclosed the stigmal plates and peritremata (Fig. 35). In young nonattenuate individuals this continuity is not apparent because the sclerotization is so feeble (Fig. 17). At the sides of the genital opening the post-coxal apodemes unite with, or are produced into, a pair of spur-like apodemes which project posteriorly (Fig. 28). Genital plate greatly variable in size and form (Figs. 43–53). A pair of rings lies either in or near the genital plate. Although variable, the genital plates of individuals from *Eumetopias jubata* are generally larger and more elliptical than in specimens from *Callorhinus ursinus.* This will be discussed below.

Setae of opisthosoma usually difficult to find in older females. Cuticle not pierced by pores of the type found in *Halarachne americana.* Portions of podosoma between coxae and dorsal plates covered by very irregular patches of a brown secretion. This is completely lacking in the youngest nonattenuate specimens; but in some of the older females virtually the entire dorsal and lateral surfaces of the podosoma are covered, although it is not deposited over the dorsal plate. Nothing is known of the nature of the secretion except that it is insoluble in alcohol, water, acetic acid, lactic acid and glycerine, but it is soluble in a dilute solution of potassium hydroxide (ca. 5%) at a temperature of 60–75° C. and hence it is not chitin. In a female with an abnormal twisted abdomen, about 20 brown concretions were seen inside the body cavity, distributed throughout its length, and seven of these were clustered on one side of a developing embryo. This apparently is the same material that is secreted on the outer surface of the body. Why it should be secreted internally is unknown, but at least this seemingly pathological case shows that the external secretion is, with little doubt, a product of the mite and not of the host.

Posterior portion of peritremalia distinct, almost completely enclosing the stigmal plate and peritreme. Ventral margin of stigmal plate characteristically exposed in all of the several specimens examined for this feature (Figs. 17, 35).

Digitus fixus of chelicera bifid, the dorsal membrane not projecting beyond the prominent, ventrally-inclined tip of tarsus (Figs. 33, 38). The general morphology of the chelicera has been discussed previously

(p. 239). Maxillary setae somewhat variable, especially the posterior pair, one of which is occasionally absent or displaced. Free portion of palpi as in male, except that trochanter does not bear a discrete process ventrally. The trochanter in Fig. 40 is probably higher than normal, owing to compression.

The lengths of the leg segments given below were obtained from a female in which the dorsal plate is 910μ long. The length of coxa + trochanter (c + tr) and of the ambulacrum (amb.) is the maximum length. In the other segments the dorsal length is given. Basifemur = bfe, distifemur = dfe, patella = pt, tibia = ti, basitarsus = bta, distitarsus = dta, total = T, ratio of the total length to the length of the dorsal plate = T/LDP.

	c+tr	bfe	dfe	pt	ti	bta	dta	amb.	T	T/LDP
I	250μ	48	114	117	117	———218———			864	0.95
II	266	48	96	122	101	67	106	93	899	0.99
III	266	48	74	125	101	67	104	101	886	0.97
IV	200	40	93	108	210	64	130	72	917	1.01

The above measurements were made from a dissected female from *Callorhinus ursinus*, Depoe Bay, Oregon (Slide no. 45–238–19). The basitarsus, distitarsus, and ambulacrum of leg I cannot be measured separately because of their structure, so only the total length is given.

Male. Total body length attaining 4500μ or more. Dimensions of dorsal plate as given for female. Essentially like female except in characters of ventral surface of podosoma and the mouthparts. The antero-lateral projections of the sternal plate shown in Fig. 42 appear to be exceptional since they are absent in other specimens, or greatly reduced. Genital opening completely anterior, or with a narrow strip of the plate anterior to opening. Opisthosoma uniformly cylindrical as in nongravid females.

Chelicerae as shown in Figs. 32 and 36, dorsal membrane of tarsus variable in length. Trochanter of palp with a discrete ventral process which is not bifid. The palp from which Fig. 37 is drawn is abnormal

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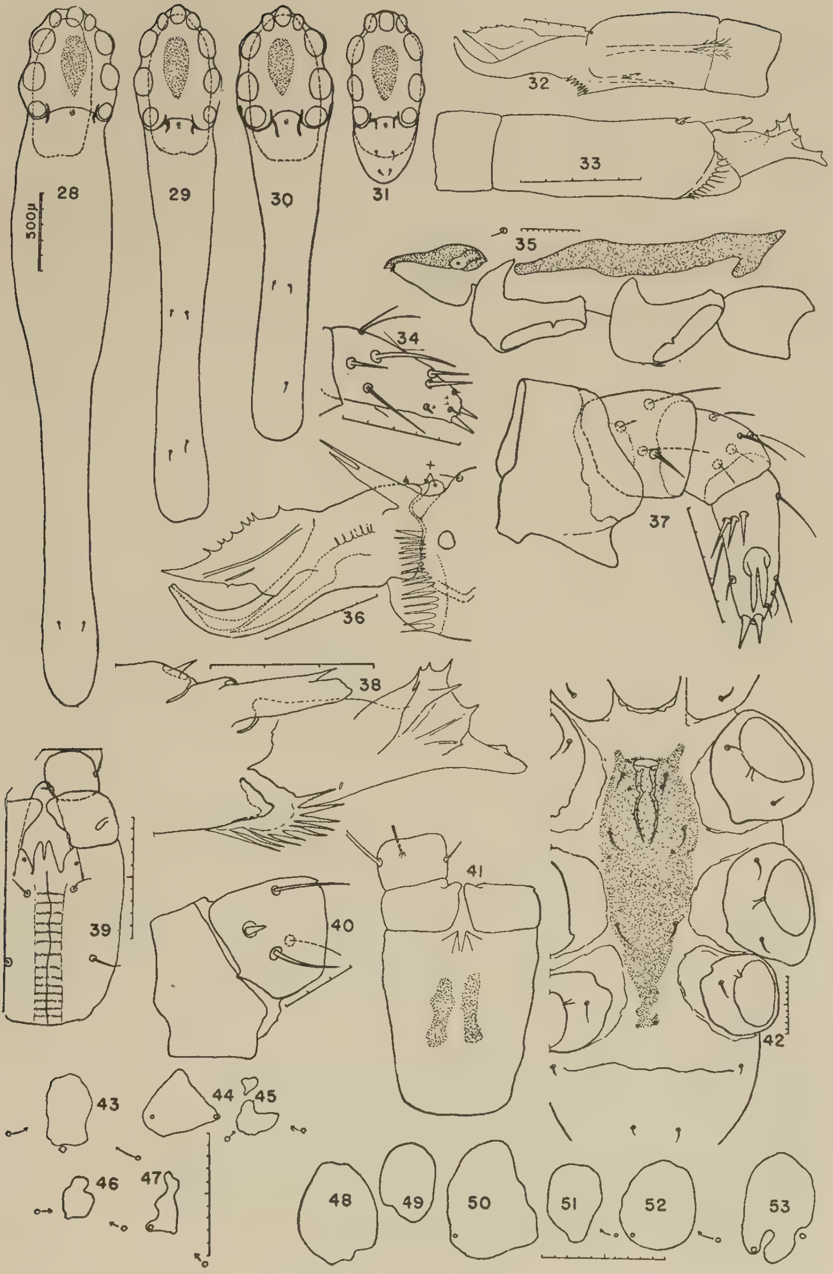
Figures 28–53. *Orthohalarachne attenuata* (continued). *28* Female (from *E. jubata;* St. Paul): venter (scale = 500μ). *29* Female: venter. *30* Female: venter. *31* Female: venter. *32* Male: chelicera, lateral view. *33* Female: chelicera, lateral view. *34* Male: tibiotarsus of palp, lateral view. *35* Male: podosoma, dorso-lateral view. *36* Male: distal portion of chelicera, median view. *37* Male: palp, median view. *38* Female: chelicera, median view. *39* Female: capitulum, ventral view. *40* Female: trochanter and femur of palp, lateral view. *41* Larva: capitulum, ventral view. *42* Male: venter. *43–47* Females (from *C. ursinus;* St. Paul): genital plate. *48–53* Females (from *E. jubata*; St. Paul): genital plate.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in that there are 5 setae on the patella (P–3). The posterior seta is absent from the opposite palp, as from both palpi of the five or six other specimens of both sexes that were examined closely for this character.

Larva. Body 1000 to 1100µ long (2 larvae). Dorsal anal seta often duplicated. No particular specific characters were observed.

Post-larval development. The development of the adult following the moult of the larval skin has long been a matter of conjecture. It has never been observed directly, and none of the authors who have published on the species of *Orthohalarachne* has been able to add much to our knowledge on the basis of preserved material. Oudemans, in 1926, could say only "Wenn ein Weibchen aus der Larvenhaut zum Vorschein kommt, ist es natürlich kurz; es wird dann, warscheinlich sehr schnell, anwachsen . . ." (Oudemans 1926d: 88, *O. zalophi*). The subject is of biological interest in itself, but it is also important because several questions of host relationship and taxonomy are related to it. For instance, Finnegan (1934: 326) pointed out the possibility that the type host record for *Orthohalarachne rosmari* is incorrect, since the type specimens were obtained from a walrus which had lived in the same basin occupied by the sea lions in Hagenbeck's Zoological Gardens in Hamburg, Germany. Finnegan stated, "One ought to add, however, that Dr. Oudemans, who described the species, is of the opinion that since the walrus and sea lions were only together for a few months 'it is scarcely admissible that in such a short time the Halarachnids of *Zalophus* should go over and propagate in the nasal cavities of *Odobaenus*'." (no reference is given by Finnegan for the quotation from Oudemans).

There is no evidence that the host record for *O. rosmari* is incorrect, but there is evidence that "a few months" is more than ample for cross-infection to occur. One of the lots of Halarachnidae collected by V. B. Scheffer was taken from a fur seal pup estimated to be two to four weeks old which was taken to the laboratory in a dying condition. The death of the seal was not caused by mite infestation, although this may have been a contributing factor, since "several dozen crawled from the nose as the pup was being examined."[6] *O. diminuata* was present here also. In all, 22 specimens of *O. attenuata* were taken from the nasal passages, 9 of which were nonattenuate (Figs. 18, 19,

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[6] Field note by V. B. Scheffer.

31) and 13 attenuate (Fig. 29). Of the latter, 8 were males and 5 were females. Each female contained an egg about 450μ long, the contents of which were densely packed and granular. There was no sign of segmentation. The longest female was 3540μ, whereas females containing larvae are 4000 to 4500μ long as a rule (body only). The base of the abdomen was not swollen as in the old females. Although these adults were no more than a month old, and possibly much less, they had bodies 80 per cent as long as in the larvigerous females, and contained eggs. The fact that host specificity appears to be weak in the Halarachnidae, in addition to the very short time required for infection and subsequent development, requires that all host records obtained from zoological park material be accepted with great reservation.

Other significant changes associated with age are: 1) an increased intensity of pigmentation, 2) deposition of the wax-like substance on the podosoma, 3) widening of the genital opening of the female, and 4) redistribution of the tracheae of the opisthosoma. With regard to the latter it must be noted that in nonattenuate females (Fig. 31) the tracheae of the opisthosoma form a knotted mass in the posterior end of the body cavity; but by the time the body has elongated to the stage shown in Fig. 30 the main longitudinal trunks have become straightened. The dorsal plate and legs of nonattenuate individuals are straw-yellow or nearly colorless, whereas in older individuals these are varying shades of brown or red-brown.

It has been realized for many years that there is no nymphal instar, although the evidence for this is only the consistent absence of nymphs. The "nymphes octopodes" of *Halarachne* sp. Blanchard 1906 must have been adults; the "nymph" of Ferris is the larva.

Variation. The specimens from *Callorhinus ursinus* are so like those from *Eumetopias jubata* that they must be considered as belonging to the same species. Evidence that subspeciation is under way is seen in the genital plate of the female, although the degree of overlapping that occurs does not seem to warrant the erection of subspecies at present. Figs. 43–47 show the genital plates of five specimens from *Callorhinus ursinus* chosen at random from specimens taken on St. Paul. Specimens from *C. ursinus* from Oregon likewise show reduced genital plates. Figs. 48–53 are of females from *Eumetopias jubata,* also chosen at random. It is not impossible, of course, that the differences in size are only ecophenotypic, resulting from host differences.

The geographical ranges of these two forms of *Orthohalarachne attenuata* overlap widely, but there is a certain amount of ecological isolation which is not perfect and apparently is not sufficiently strong, or the genetic stability of the species is too great, for clear-cut subspeciation to occur. It is not advisable to give names to these apparent semi-isolated breeding populations at present. The character of the genital plate is one which is purely relative, and parallel reduction could occur in populations which are only remotely related to one another. Accordingly, a situation could easily arise wherein two separate populations are placed together under one name, whereas they are less closely related to each other than to the original stock.

2. *Orthohalarachne reflexa* (Tubb) 1937

Tubb 1937, 417–418: *Halarachne reflexa*, sp. nov.

Distribution. Lady Julia Percy Island (ca. 38° 25′ S., 142° 3′ E.).

Remarks. The status of this form is uncertain at present, but it seems unlikely that it is a distinct species. Specimens collected by J. A. Tubb at the type locality in January of 1936 were kindly sent by Herbert Womersley of the South Australian Museum to V. B. Scheffer who in turn sent them to the writer for study. The lot contained nine females which could not be distinguished from females of *Orthohalarachne attenuata* taken from *Callorhinus ursinus* in the Pribilof Islands. Complete agreement is found in the extreme reduction of the genital plate and in the duplication of the median anal seta of some specimens. It is possible that further study, especially of males, will reveal differences of at least subspecific value, and therefore the name is retained here rather than being declared a synonym of *Orthohalarachne attenuata.*

3. *Orthohalarachne zalophi* (Oudemans) 1916

Oudemans 1916f, 312: *Halarachne zalophi* nov. sp. Steding 1923, 442–493: *Halarachne Otariae* n. sp. Oudemans 1926d, 50, 85–95, 98, 107–108: *Halarachne zalophi* Oudms. 1916. Finnegan 1934, 324, 326: *Halarachne zalophi* Oud. Ass 1935, 602: *Halarachne otaria* Steding. Doetschman 1941, 23: *Halarachne zalophi* Oudemans. Ferris 1942, 78, 79, 83: *Halarachne zalophi* Oudemans 1916. Doetschman 1944, 70: *Halarachne zalophi* Oudemans 1916.

Distribution. California (Pacific Grove, ca. 36° 38′ N., 122° W.; and San Diego, ca. 32° 45′ N., 117° 15′ W., in zoo).

Hosts. *Zalophus californianus* (Lesson) (= *Otaria californica*). *Eumetopias jubata* (zoo specimens). (Otariidae)

Remarks. The types of both *Halarachne otariae* Steding 1923 and *Orthohalarachne zalophi* (Oudemans) 1916 probably came from the same much-studied sea-lion head, and accordingly *H. otariae* is a synonym of *O. zalophi.* Steding's work was important from an internal anatomical standpoint, but her description of *H. otariae* contained no reliable features which enable us to distinguish two species. The possibility of synonymy was first mentioned by Finnegan (1934: 324) and was reviewed more in detail by Ferris (1942: 79). Ferris also noted the "strong possibility" that *O. zalophi* was identical with *O. attenuata,* and the present writer feels that this may eventually prove to be true. Judging from the large size of the genital plate of *O. zalophi* (see Ferris 1942: 83), it would resemble most closely the forms taken from *Eumetopias jubata* on St. Paul Island. However, it may represent a third semi-isolated population of *O. attenuata.*

Oudemans (1926d: 89) showed the third pair of sternal setae outside the plate, whereas in *O. attenuata* they are in the margin of the plate. His specimens were mounted in balsam, however, and it may have been that the margin of the plate was so transparent that it could not be seen. The writer has examined balsam mounts of *O. attenuata* in which it is impossible to discern the actual margin of the plate under any magnification or condition of lighting, and the same may have been true in the specimens seen by Oudemans. The fact that in a gravid female the third pair of setae remain less widely separated than the second (Oudemans 1926d: fig. 40) would suggest that they were still firmly held by the plate. In *Halarachne americana* this is not the case (Figs. 10, 13), and the posterior setae become more widely separated with distention of the body.

Ferris (1942: 79) stated, "Attention should be called to the strongly sclerotized and acute epistomal process and to the fact that the ventral side of the capitular base, which is composed of the fused palpal bases, bears two pairs of quite large setae and shows no trace of the lobes which appear in *halichoeri.*" The "lobes" are the malae exteriores which were unquestionably present in Ferris' material. They are much too conservative structures to be lost in this form, which is probably no more than subspecifically distinct from *O. attenuata,* if that (compare Figs. 5, 20, 39, 65). Ferris' drawing of the chelicera is not to be compared with the figures of *O. attenuata* in this paper, since it was drawn from a different view.

4. *Orthohalarachne rosmari* (Oudemans) 1916

Oudemans 1916f, 312: *Halarachne rosmari* nov. sp. Finnegan 1934, 321, 323–326: *Halarachne rosmari* Oudemans. Ferris 1942, 78: *Halarachne rosmari* Oudemans 1916.

Distribution. ? Franz-Joseph Land (ca. 81° N., 60° E.).

Host. ? *Odobenus rosmarus* (Linnaeus) (Odobenidae).

Remarks. This species was described from a walrus that had lived in a zoological park in Hamburg for seven years after it was collected in Franz-Joseph Land. On the basis of Oudemans' description and illustrations it appears to be distinct. The difference in form of dorsal plate in the male and female is exceptional, if accurately represented.

5. *Orthohalarachne magellanica* (Finnegan) 1934

Finnegan 1934, 321–326: *Halarachne magellanica* sp. n.

Distribution. Falkland Islands (ca. 52° S., 60° W.).

Host. *Otaria byronia* (de Blainville), "Southern Sea Lion" (*Otariidae*).

Remarks. Significant diagnostic characteristics of this species appear to be the relative shortness of the dorsal plate (L/W = 1.75–1.8) and the greatly enlarged trochanter of the male palp.

6. *Orthohalarachne diminuata* (Doetschman) 1944.

Doetschman 1941, 23: "new species" (no name given). Doetschman 1944, 68–72: *Halarachne diminuata* n. sp.

Distribution and Hosts. *Zalophus californianus* "California Sea Lion" (Otariidae); California. *Callorhinus ursinus* "Alaska Fur Seal" (Otariidae); St. Paul Island (57° 5′ N., 170°, 25′ W.).

Diagnosis. With all the generic and family characters listed above, in addition to the following.

Female: The two females have bodies 697 x 337μ (L/W = 2.06) and 809 x 416μ (L/W = 1.94). Whether the abdomen becomes attenuate in older adults is not known, but it probably does not. Some of Doetschman's specimens, which were even larger than those seen by

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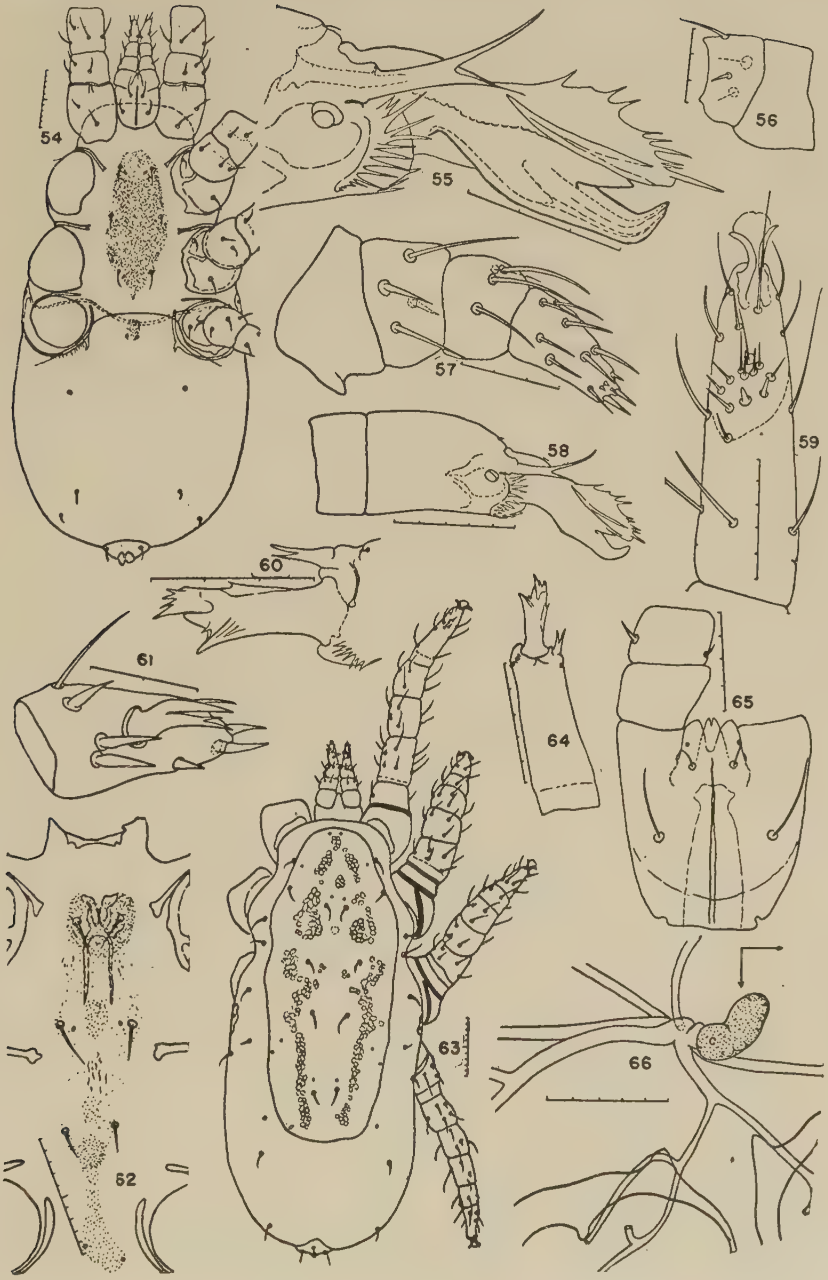
Figures 54–66. *Orthohalarachne diminuata* (Doetschman) 1944. All from *Callorhinus ursinus*, St. Paul Island. *54* Female: venter. *55* Male: distal portion of chelicera, median view. *56* Female: trochanter and femur of palp, median view. *57* Male: palp, lateral view. *58* Male: chelicera, median view. *59* Female: tarsus I, dorsal view. *60* Female: distal portion of chelicera, lateral view. *61* Male: tibiotarsus of palp, median view. *62* Male: venter. *63* Female: dorsum. *64* Female: chelicera, lateral view. *65* Adult: capitulum, ventral view. *66* Male: peritreme, stigmal plate and tracheae of left sides, lateral view.



the writer, showed no evidence of attenuation. Doetschman did not say whether any of the females contained embryos; those seen by the writer do not.

Dorsum (Fig. 63): dorsal plate 562 x 236μ (L/W = 2.38) and 575 x 242μ (L/W = 2.38). Using 900μ as the total length of the specimen shown by Doetschman (1944: fig. 1), the dorsal plate of his specimen is about 563μ long. Setae of dorsal plate conspicuous, 10 in number, other setae, pores and muscle insertions as shown in Fig. 63. Eight pairs of setae lie in the dorsal membranous area, making a total of 13 pairs of dorsal setae. There are usually 14 pairs in *O. attenuata*. The refractile rings near the postero-lateral angles of the dorsal plate are very near the position of the missing pair and may represent the vestigial insertion of these (compare Fig. 63 with Fig. 18).

Tritosternum lacking in both specimens. Sternal plate very faint, somewhat irregular in outline, appearing (in glycerine) as a faintly stippled area. In well digested material, at a magnification of 950 or greater, it can be seen that all 6 sternal setae lie within the plate, with the second pair more widely separated than the third pair. In one of the females the plate is rounded behind the third pair of setae, not pointed as shown in the figure. A pore lies behind only the first 2 pairs of setae. Stigma between and above coxae III and IV. Peritremalia (not shown in figures) as in *O. attenuata*, but extremely faint, especially the posterior portion surrounding the stigmal plate and peritreme. Four pairs of band-like post-coxal apodemes present. Delicate internal hair-like processes on apodeme IV show where muscles are attached. Apodeme IV continuous with posterior portion of peritremalia. Genital plate minute, with a pair of refractile rings which may represent the vestiges of setal insertions; setae absent in genital region. Another pair of refractile spots posterior to coxae IV. Anal plate completely terminal, dorsal anal seta showing no tendency toward duplication.

Chelicera (Figs. 60, 64) with dorsal membrane of digitus mobilis directed anteriorly and reaching beyond the heavy, ventrally-inclined tip. Digitus fixus bifid. Dorsal seta at base of digitus fixus so small it could scarcely be resolved, even at a magnification of 1600x. Palpi as in male, except for absence of the ventral apophysis on segment I (trochanter) and slightly smaller size (Fig. 56). Ventral surface of capitulum typical of the genus.

No particular specific characters were noted in the legs. Certain of the setae on the antero-dorsal surfaces of the segments are short and stout (Fig. 63), as in *O. attenuata.*

Male: Dorsal plate 562 x 254μ (L/W = 2.21); essentially as in female. Body alone 629 x 393μ (L/W = 1.60). Sternal plate virtually invisible at low magnifications. Under oil immersion, however, it is seen that a faint sternal plate with few scattered punctae is present, and this includes all 3 pairs of sternal setae. Two pairs of pores associated with the 4 anterior sternal setae; a pair of refractile rings at posterior end of plate between coxae IV. Differences in distribution of the punctae are shown in Fig. 62. Chelicerae and palpi as shown in Figs. 55, 57 and 61. The constancy of the bifurcation of the ventral digit of the tarsal prong (Fig. 61) is unknown. Leg I 540μ long, .96 as long as dorsal plate.

Remarks. There is no question that these two females and the male belong to this species. Considering that the specimens were taken from a different host, and even from a different zoogeographic province, it would be permissible to anticipate subspecific differences. Unfortunately the original description is not sufficiently detailed or accurate to permit a close comparison.

Doetschman made a comparison of the species only with *Halarachne americana*, stating, "There are many resemblances between *H. diminuata* n. sp. and *H. americana* Banks 1899." But this resemblance is artifical, consisting mainly of a somewhat similar body form and size, for there are 10 or 12 absolute characters listed in the generic diagnosis above in which the species differs from *H. americana*, while it shares every one of these characters with *Orthohalarachne attenuata*. Even the correspondence in size is fundamentally misleading, for *H. americana* is really larger than *O. attenuata*, despite the fact that it is shorter. The following measurements of representative specimens demonstrate this (all in micra):

	H. americana	*O. attenuata*	*O. diminuata*
Body length	2800μ	4500μ	740μ
Length of opisthosoma behind dorsal shield	1380	3500	190
Dorsal plate	1400	930	560
Length of podosoma	950	700	425
Diameter of coxa III	300	215	115
Max. width podosoma	1050	650	330
Max. width opisthosoma	1400	650	330

In all measurements but length of opisthosoma and total body length, *H. americana* exceeds *O. attenuata*, and thus *O. diminuata* more nearly resembles *O. attenuata* even in the relative character of size. This also demonstrates how misleading the single measurement, body length, can be. It is clear that *O. diminuata* is not to be compared with *H. americana*, but only with species of *Orthohalarachne*.

Genus *Pneumonyssus* Banks 1901

Oudemans (1935b) reviewed this genus and listed five species which he considered valid. Further reference to these can be found there. Subsequently, two new species have been placed here, so that the list is as follows:

1. *P. simicola* Banks 1901. Genotype.
2. *P. duttoni* Newstead *et* Todd 1906.
3. *P. congoensis* Ewing 1929.
4. *P. stammeri* Vitzthum 1930.
5. *P. dinolti* Oudemans 1935.
6. *P. procavians* Radford 1938.
7. *P. caninum* Chandler *et* Ruhe 1940.

Synonym. *Pneumotuber* Landois *et* Hoepke 1914. The genotype of *Pneumotuber* is *Pneumotuber macaci*, which is identical with *Pneumonyssus simicola*. The latter names have priority.

Remarks. The genus *Pneumonyssus* as it now stands will almost certainly require revision, since it apparently includes species of diverse phylogenetic origin. But although it seems unlikely that the genus is monophyletic, there is a considerable degree of morphological uniformity which is difficult to evaluate on the basis of present descriptions of the species, nearly all of which are inadequate if not inaccurate in several critical points. This morphological uniformity probably arises from two distinct causes, namely that (1) the habitats of the various species are similar, consisting of the respiratory tracts of various mammals, and (2) all of the species probably arose from species of external parasites which today would be placed in or near the families Liponyssidae or Laelaptidae. In other words, the predecessors of the present day *Pneumonyssus* species were all closely related both ecologically and systematically. The difficulties in the way of developing a system of classification that is both natural and convenient will be readily apparent to most workers in biology.

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Contribution No. 355

A SUMMARY OF THE THEORY OF CONVECTION CELLS

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INTRODUCTION

When a horizontal layer of viscous fluid is uniformly heated from below, a steady regime may occur in one of the following two ways. If the temperature difference between the two horizontal bounding surfaces is sufficiently small, the heat supplied at the bottom surface may be delivered to the top surface by conduction alone, in which case no fluid motion occurs. For greater temperature differences, the fluid assumes a convective motion, which occurs in a very regular cell-like pattern. The entire layer divides itself up into self-contained identical cells whose convective circulation transfers heat from the bottom to the top surface.

The experimental and theoretical studies of convection cells that have been made to date have essentially been efforts to discover: (1) the critical temperature gradient at which the steady regime changes from one of conduction to one of convection; and (2) the geometry and dimensions of the cells that are formed in the convective state.

EXPERIMENTS

The chief source of experimental data is the work of Henri Benard.[1] Briefly, his procedure was as follows: He heated a horizontal layer of fluid from below, and noted the formation of polygonal cells in a more or less regular pattern, also that there were certain "laws" which govern the dimensions and shape of the cells. Dr. Paul Queney, of the University of Paris and the University of Algiers, tells the author of some interesting elaborations of convection cell experiments which he saw performed in Benard's laboratory. In these, a thin layer of a non-electrolyte was electrostatically charged, positively on the top surface and negatively on the bottom surface, and the resulting convection studied. At an even earlier date, the same tessellated structure was noticed by J. Thomson,[2] during the cooling from above of soapy fluids.

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* Contribution No. 355.

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FIELD OBSERVATIONS

As early as 1862, J. Thomson noticed sinuous markings and calm areas on the sea, and suggested that they were due to vertical cellular circulation.[3] Irving Langmuir[4] made numerous measurements of the streaks and lines appearing upon Lake George. A. H. Woodcock[5] studied the wind-induced motion of *Physalia,* and also made a number of drift bottle measurements to determine the nature of the surface flow in convective strips in the open sea and, in particular, any possible asymmetry due to the earth's rotation.

In all three of the preceding cases, long, parallel convection strips were considered, instead of simple regular cells.

On Erdmann's Tundra, Spitzbergen, there appear wide stretches covered with stones arranged in rough polygons. The transport and arrangement of these stones has been explained as due to the cellular convection cells presumably set up in soil water during the thaws.

A. R. Low[6] and D. Brunt[7] suggest that the concept of the convection cell might prove an important tool for the understanding and description of such phenomena as multiple thunderstorms, etc. Mal,[8] and Phillips and Walker,[9] attempted to interpret various cloud forms in terms of convection cells.

Recent studies of convective motion in the atmosphere have been made by Dr. Jeffries Wyman, A. H. Woodcock, and others, for the U. S. Navy Department. They will be discussed separately.

THE AVAILABLE THEORETICAL LITERATURE

The basic approach to the theoretical treatment of the problem of the stability and geometry of convection cells was made in 1916, by Lord Rayleigh.[10] Several other treatises have appeared since that time,[11-13a] but they are all essentially refinements and rephrasings of his original work. These will be referred to repeatedly throughout the rest of this paper. The authors vary somewhat in their respective treatment of the problem, and in the notation they use. In the following, an attempt will be made to outline the theory in general and, at the same time, to point out how and where each author's treatment differs from that of another.

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THE DIFFERENTIAL EQUATIONS

The basis of all the theories propounded is provided by the following three equations:

(a) Euler's equation of motion;

(b) Equation of continuity;

(c) Equation of thermal diffusion.

Our task becomes one of making certain simplifying assumptions, so that we may finally construct a simple analytical solution of the three equations taken simultaneously. We must also succeed in imposing certain boundary conditions, without which the equations bear no resemblance to the physical problem.

First, let us turn to the unsimplified equations themselves.

(a) *Euler's Equation of Motion:*

$$\rho \frac{D\mathbf{v}}{Dt} = \rho\mathbf{F} - \nabla p' + \frac{1}{3} \nu\rho\nabla\nabla \cdot \mathbf{v} + \nu\rho\nabla^2\mathbf{v} + \rho\mathbf{v} \times 2\omega,$$

where ρ is the density,

$\frac{D}{Dt}$ the substantial derivative,

$\mathbf{v}$ the vector velocity,

$\mathbf{F}$ the external force field,

∇ the nabla operator,

p' the pressure,

ν the coefficient of kinematic viscosity,

∇^2 the Laplacian operator, and

ω the vector rotation of the earth.

We have assumed that the x, y, z axes are so chosen that the origin is at the bottom of the layer and z points upward.

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(b) *Equation of Continuity:*

$$\frac{D\rho}{Dt} + \rho \nabla \cdot \mathbf{v} = 0.$$

(c) *Equation of Thermal Diffusion:*

$$\frac{D\vartheta'}{Dt} = \kappa \nabla^2 \vartheta',$$

where ϑ' is the temperature, and
κ the coefficient of thermal diffusivity.

SIMPLIFYING ASSUMPTIONS

The following simplifying assumptions are made:

(1) The fluid is incompressible, the density ρ constant, except for its thermal expansion, as it modifies the gravity term.

(2) The temperature gradient in the steady state is linear.

(3) The thermal expansion is linear.

(4) The motion is so slow that u, v, and w, the components of $\mathbf{v}$, are small enough so that their products and squares are negligible in a first approximation.

(5) $\omega = 0$ in all papers except Jeffries,[11a] where the vertical component is considered qualitatively.

(6) κ and ν are true constants. In meteorological problems, the variable eddy diffusivity and viscosity would be much more significant. For example, it would be interesting to carry through a solution where κ and ν are linear functions of z.

THE APPROXIMATE DIFFERENTIAL EQUATIONS

By virtue of the foregoing assumptions, the three basic equations are much simplified, as shown:

(a) *Modified Form of Euler's Equation of Motion:*

$$\left(\frac{\partial}{\partial t} - \nu \nabla^2\right) \mathbf{v} = -\frac{1}{\rho} \nabla p + \epsilon \gamma \vartheta,$$

where ϵ is the unit vector in the z direction,
g the acceleration of gravity,
α the coefficient of thermal expansion and $\gamma = \alpha g$,
ϑ the deviation of the temperature ϑ' from that of the steady state ϑ_0, and
p the deviation of the pressure p' from that of the steady state p_0.

(b) *Modified Equation of Continuity:*

$$\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} + \frac{\partial w}{\partial z} = 0.$$

(c) *Modified Equation of Thermal Diffusion:*

$$\left[\frac{\partial}{\partial t} - \kappa\nabla^2\right]\vartheta = -\beta w,$$

where

$$\beta \text{ is } \frac{\partial\vartheta'}{\partial z}.$$

To solve these equations simultaneously, one cross-differentiates and eliminates u, v, p, ϑ and obtains a partial differential equation of the sixth order in w:

$$\left(\frac{\partial}{\partial t} - \kappa\nabla^2\right)\left(\frac{\partial}{\partial t} - \nu\nabla^2\right)\nabla^2 w + \beta\gamma\nabla_1^2 w = 0,$$

where

$$\nabla_1^2 = \frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2}.$$

Alternatively, it is possible to develop the equations in terms of ϑ.[11, 11a]

SOLVING THE PARTIAL DIFFERENTIAL EQUATION IN *w*

The solution of the partial differential equation is assumed to be separable into functions of x, y, z, and t. We may express this by writing

$$w = Wf(x, y)F(z)\Phi(t).$$

Our solution then takes a form in which the factor $f(x, y)$ depends upon the lateral geometry of the cell, the factor $F(z)$ is determined by the top and bottom boundary conditions, and the factor $\Phi(t)$ determines the stability of any particular regime. We will now proceed to examine each of these factors separately.

THE *f*(*x*, *y*) FACTOR

Until now, assumptions have been made about the existence of cells. In discussing the factor $f(x, y)$, we implicitly assume their existence. Their nature (shape, etc.) will depend upon our particular choice of $f(x, y)$. The theoretical method, however, does not indicate which shape of cell will actually form. For practical purposes, we may limit ourselves to simple geometric forms such as the square, the infinite strip, and the hexagon. Because we are in effect dealing with a problem of plane tessellation, a few elementary remarks may be appropriate.*

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* For a more detailed discussion, see: **Kraitchik, M.** La Mathématique des Jeux. Brussels. 1930.

A plane tessellation may be made in an unlimited number of ways, if no restriction is placed upon the size and shape of the geometrical forms making up the pattern. In a definite pattern, as in convection cells, certain restrictions are imposed. Suppose we restrict the tessellation to one in which all the components are identical regular polygons, each with n sides. Consider a point P at which we wish to join the vertices of m, say, of these n-polygons. Each of the n-polygons has an interior angle of $(n-2)\pi/n$. If the point P is to be entirely surrounded, then $m \cdot (n-2)\pi/n = 2\pi$, or $(m-2)(n-2) = 4$. Both $m, n > 2$. We need only consider the cases:

$$\begin{array}{ll} n = 3, & m = 6, \\ n = 4, & m = 4, \\ n = 5, & m \text{ not an integer}, \\ n = 6, & m = 3. \end{array}$$

Therefore, the plane may be tessellated by identical regular polygons only in cases where the polygons surrounding the point P are (a) six equilateral triangles; (b) four squares; or (c) three hexagons. If combinations of polygons are permitted, eight other possible cases arise, but these are of little importance for practical purposes.

a. Rectangular Cells[10, 11, 11a]

If $f(x, y)$ is of the form of $e^{ilx}e^{imy}$, the cells are rectangular, their sides parallel to the x and y axes, and with sides of the length $2\pi/l$, $2\pi/m$. Analytically, this is the simplest form of solution possible. In the case $l = m$, the cells are squares. If either $l = 0$ or $m = 0$, but not both, the cells are infinitely long strips.

b. Hexagonal Cells[12]

Due to the discovery, by D. G. Christopherson,[14] of an exact functional solution for the hexagonal cell, we are now able to examine this important case. Cells produced experimentally are, after an initial transient state in which 4- and 7-sided polygons are present, generally hexagonal. The Christopherson function is of the form:

$$f(x,y) = \frac{1}{2} w_0 \left\{ \cos \frac{2n\pi}{3L} (\sqrt{3}\,x + y) + \cos \frac{2n\pi}{3L} (\sqrt{3}\,x - y) + \cos \frac{4n\pi}{3L} y \right\},$$

where L is the length of a side of the hexagon and w_0 the value of w at the center of the hexagon.

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[14] Quart. J. Math. **11**: 63–65. 1940.

c. Circular and Nearly Circular Cells

Before Christopherson's discovery, an attempt was made[10] to approximate the hexagon by small deviations from the circular case which, in turn, may be developed in terms of Bessel functions. The method appears in an appendix of Rayleigh's paper[10] and is developed fully in his *Theory of Sound*. With the discovery of the exact functional solution for the hexagonal cell, this treatment assumes less practical importance.

d. Triangular Cells

These may be developed in terms of the hexagonal solution.

e. Elliptic Cells

Solutions for cells with elliptical boundaries may be developed in terms of Mathieu functions. However, no such solution has been made, presumably because the case is of little physical interest.

f. The *a* Parameter[12]

It is possible to sidestep the issue of the exact functional form of $f(x, y)$ by the introduction of a parameter a. This is possible because the nature of $f(x, y)$ is such that $f(x, y) \propto \Delta_1{}^2 f(x, y)$. We impose the condition:

$$h^2\nabla_1{}^2 w + a_2 w = 0,$$

in which h is the depth of the cell and a^2 is a characteristic number as yet undetermined.

The parameter a may be carried through the solution formally and its final significance for certain definite shapes determined numerically.

g. The $F(z)$ Factor

The factor $F(z)$ depends upon the nature of the top and bottom surfaces. Except in one study,[13a] it is assumed that every cell extends all the way from the top to the bottom of the layer. We assume that, at the boundaries, the temperature is everywhere the same, so that on them, $\vartheta' = \vartheta_0$ or $\vartheta = 0$. At a free surface, $w = \dfrac{\partial^2 w}{\partial z^2} = 0$; at a rigid boundary, $w = \dfrac{\partial w}{\partial z} = 0$. TABLE 1 illustrates the possible cases and names the authors who have treated them.

The particular form assumed by Rayleigh is $F(z) = \sin \dfrac{r\pi}{h} z$, where r is an integer.

TABLE 1

			Top			
			Rigid		Free	
			Conducting	Non-conducting	Conducting	Non-conducting
Bottom	Rigid	Conducting	**Jeffreys**[11,11a] **Pellew & Southwell**[12]		**Pellew & Southwell**[12]	**Jeffreys**[11,11a]
		Non-conducting		**Jeffreys**[11a]		
	Free	Conducting	**Pellew & Southwell**[12]		**Rayleigh**[10] **Pellew & Southwell**[12]	
		Non-conducting				

THE $\Phi(t)$ FACTOR

The most important single point about the $\Phi(t)$ factor is its exponential character. Consider any quantity $q \propto e^{nt}$. If n is in general complex, the following deductions may be made concerning the stability of q:

If $\mathfrak{I}(n) \neq 0$, the motion of q is oscillatory; if $\mathfrak{I}(n) = 0$, there is no oscillation. If $\mathfrak{R}(n) = 0$, the oscillation of q is of steady amplitude; if $\mathfrak{R}(n) \neq 0$, the amplitude of the oscillation changes: in particular, if $\mathfrak{R}(n) < 0$, it decreases, or if $\mathfrak{R}(n) > 0$, it increases. If both $\mathfrak{I}(n) = 0$ and $\mathfrak{R}(n) = 0$, then q is a constant.

If, after a small displacement δq of q from the steady state value q_0, q gradually returns to q_0, the physical regime which q describes is said to be stable. If, on the other hand, q becomes indefinitely great, upon the introduction of a small displacement δq, the regime is unstable. Instability, that is, convective motion, arises if, and only if, $\mathfrak{R}(n) > 0$. The application of this stability criterion[10] on w is possible, provided:

$$\Phi(t) = e^{nt}.$$

COMBINATION OF THE FACTORS AND DETERMINATION OF THE STABILITY CRITERION

Essentially, then (in this paragraph we follow Rayleigh), one constructs a function for w by combining the features of $f(x, y)$, $F(z)$, and $\Phi(t)$ which apply to the case under investigation. This form of w is then substituted into the partial differential equation in w. The result is an algebraic relation among the physical parameters β, γ, κ, ν, the geometric elements (*e.g.*, l, m, h) of the cell, and the quantity n. This algebraic relation may be regarded as a polynomial in n, the roots of which are then investigated in the light of the stability criterion (that for instability $\mathfrak{R}(n) > 0$). Certain inequalities arise among the physical parameters and geometric elements of the cell, which are, in fact, the conditions for stability or instability. For example,[10] if κ, ν, γ β are defined as above, and if we consider a rectangular cell of sides $\frac{2\pi}{l}$ and $\frac{2\pi}{m}$ in a liquid of depth, we assume a form of solution:

$$w = We^{ilx}e^{imy}e^{nt} \sin sz,$$

where $$s = \frac{r\pi}{h}, \qquad r = 1, 2, 3, \ \ldots,$$

and substitute it into the differential equation. The result is an algebraic equation in n:

$$(n + \kappa\sigma)(n + \nu\sigma)\sigma + \beta\gamma(l^2 + m^2) = 0,$$

where $$\sigma = l^2 + m^2 + s^2,$$

whose roots have positive real parts when, and only when,

$$-\beta\gamma(l^2 + m^2) > \kappa\nu\sigma^3.$$

This is the condition for convection motion for cells of a particular size. To quote Rayleigh: "It is of interest to inquire at what point the equilibrium becomes unstable (*i.e.* the regime becomes convective) when there is no restriction upon the value of $l^2 + m^2$.

In the equation

$$-\beta\gamma(l^2 + m^2) - \kappa\nu\sigma^3 = -\beta\gamma(\sigma - s^2) - \kappa\nu\sigma^3 = 0,$$

we see that the left hand member is negative if $l^2 + m^2$ is small, and also when it is large. When the conditions are such that the equation can only just be satisfied with some value of $l^2 + m^2$, or σ, the derived equation

$$-\beta\gamma - 3\kappa\nu\sigma^2 = 0,$$

must hold good also, so that:

$$\sigma = \frac{3}{2}s^2, \qquad l^2 + m^2 = \frac{1}{2}s^2,$$

and

$$-\beta\gamma = \frac{27\kappa\nu s^4}{4}.$$

Unless $-\beta\gamma$ exceeds the value given above, there is no instability (no convective motion) no matter how l and m are chosen. But the equation contains s which may be as large as we please. The smallest value of s is $\frac{\pi}{h}$. The condition of instability, when l, m, and s are all unrestricted, is accordingly:

$$-\frac{\beta\gamma h^4}{\kappa\nu} > \frac{27\pi^4}{4} \cong 657.5.$$

If $-\beta\gamma$ falls below this amount the equilibrium is altogether stable (no convection)."

Rayleigh then proceeds to investigate the problem of the size of the cells formed:

"In an experiment the temperature gradient could not be established all at once and we may suppose the process to be very slow. In earlier stages the equilibrium would be stable (no convection; conduction only) so that no disturbance of importance would occur until n passed through zero to the positive side (that is when the thermal gradient β reached the critical value given above). The breakdown then occurs for $s = \frac{\pi}{h}$ or $l^2 + m^2 = \frac{1}{2}s^2 = \frac{\pi^2}{2h^2}$. And since the evanescence of n is equivalent to the omission of $\frac{\partial}{\partial t}$ in the original equations the motion thus determined has the character of a steady motion (steady convective regime with cells of known dimensions)."

It was mentioned above that Rayleigh's development treats only one special case, namely, that in which the top and bottom boundaries are free and the cells rectangular. Other developments[12] were shown to be possible involving a variety of boundary conditions. TABLE 2 has been computed as a final summary of the theoretical results. It gives the dimensions of complete cells that will occur in the steady convective regime. The quantity L is the side of a square cell, the width of a strip cell, or the side of a hexagonal cell, respectively.

The theory contains two rather startling implications: (1) that the geometry of the cells L/h is independent of the physical parameters; and (2) that the critical number $-\beta\gamma h^4/\kappa\nu$, which divides the case of

TABLE 2

Boundaries/cell shape	L/h			$\frac{-\beta\gamma h^4}{\kappa\nu}$
	Square	Strip	Hexagon	
Two free	4.00	2.83	1.89	657.5
One free, one rigid	3.28	2.34	1.56	1100.7
Two rigid	2.8	2.00	1.34	1707.8

steady conduction from that of steady convection, is independent of the assumed geometry of the cell.

FURTHER REMARKS

Helmholtz, in his memoir on rotational motion,[15] showed that, in a closed, simply connected space with fixed walls full of liquid, a non-constant velocity potential cannot exist. Hence, in a convection cell, which may be regarded as such a space, at least some portion of its fluid moves rotationally, if it moves at all. The functional form of solution proposed by Rayleigh, for example, may be investigated and found to demand vorticity throughout the cell.

Because the dimensions of the cells which occur in the steady convective state are independent of the physical parameters involved, one is tempted to attack the problem of their determination by using a simplified vortex model, without any reference to viscosity, temperature, etc.

The author attempted such an approach. By confining the problem to the case of infinite strip cells, it becomes two-dimensional. Further, if the vortex motion of the cells is arbitrarily confined to singular points, the problem may be formulated in terms of a complex velocity potential, specifically the logarithm of a quotient of *theta* functions. The treatment is similar to Rosenhead's treatment of the stability of a bounded Karman vortex street.[16] The result so obtained is that the model is unstable for values of $L/h < 1.416$. No upper limit of L/h is determined. Although this is not as restrictive as Rayleigh's result, the two are not mutually contradictory. Of course, the model used in this solution is very different from that of Rayleigh.

Another point of interest is the effect of the earth's rotation upon the stability of the heated fluid layer. The author preserved the rotation terms in the original equations of motion, and obtained one eighth-order partial differential equation in w and a cubic in n. The net result of the earth's rotation is to tend to prevent convective motion, especially convective motion in cells elongated in the East-West direction. Moreover, rotation effects are shown to be negligible in layers whose depth is less than about $\left(\frac{\nu}{\omega}\right)^{1/2}$.

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[15] Über Integrale der hydrodynamischen Gleichungen welche den Wirbelbewegungen entsprechen. Crelle lv. 1858.

[16] **Rosenhead, L.** Phil. Trans. Roy. Soc. A. **228:** 275. 1929.

An explanation of the direction of the circulation in cells, predominantly up in the center of liquid cells and down in the middle of gaseous cells, seems desirable. The following mechanism is suggestive: It is readily seen that, in the case of infinite strips, the direction of circulation is a question without meaning, for then one cannot speak of the outside or inside of a cell. However, in the case of cells everywhere bounded in the horizontal, there is clearly a center. A study of the flow on the bottom, or top, surface layer indicates that the greatest fluid velocities will be nearer to the center than to the outer walls. However, the viscosity of the fluid, as affected by temperature, changes mostly at the edges of the cell, where the velocity is smallest. Therefore, the total frictional resistance of the fluid motion against the bottom will be predominantly affected by the viscosity of warm fluid if the motion is upwards in the center, or by the viscosity of cool fluid if the motion is down in the center. It is reasonable to suppose that the actual regime that will be established will be that in which the total frictional resistance is smallest. In a fluid where viscosity increases with temperature, the least total resistance occurs with downward central motion; in a fluid where the viscosity decreases with temperature, with upward central motion. This, however, is known to be the general case for both gases and liquids.

In conclusion, it may be worth while to indicate some problems which the present theory does not treat or explain:

(1) the effect of variable eddy diffusivity and viscosity;
(2) the effect of compressibility;
(3) the effect of the earth's rotation on the symmetry of cells; and
(4) an explanation of why hexagonal cells predominate.

Contribution No. 356

CONVECTIVE MOTION IN AIR OVER THE SEA*

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INTRODUCTION

It has long been known that, when a confined sheet of fluid is heated from below, it becomes unstable and there develops in it a systematic pattern of circulation. The classical experiments of Benard,[1] performed nearly 50 years ago, deal with liquids. Benard found that, if a thin layer of liquid, usually free at its upper surface, is heated uniformly at the lower surface, there sets in a regime of polygonal convection cells as soon as a certain critical temperature gradient is reached. The walls of these cells are vertical, and the movement of the liquid is upward in the center and downward at the periphery. At first, the pattern is somewhat irregular, the polygons formed by a horizontal section through the cells being of different sizes and the number of sides varying from 4 to 7. After a period of time, however, ranging from one or two seconds to many minutes, depending on the viscosity of the liquid, a much more regular condition is established, in which the polygons approach regular hexagons. The relative dimensions of the cells vary somewhat with the conditions of the experiment, but the ratio of the length of the side of a hexagon to the cell height, *i.e.*, the thickness of the layer, is in the neighborhood of 2. Estimates of the velocities involved were made on the basis of observations of minute suspended particles. These showed that the horizontal components of the motion are along radii from the centers of the hexagons, and that the downward vertical motion is a maximum along the edges common to three adjacent cells, represented in horizontal section by the vertices of the hexagons. When the liquid is subjected to shear, as a result of horizontal motion, the vertical cells are replaced by horizontal strips, or double rolls, with axes parallel to the direction of shear.

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* This work represents one of the results of research carried out by the Woods Hole Oceanographic Institution, under contracts with the Bureau of Ships, Navy Department.

† Contribution No. 356.

[1] **Benard, H.** Rev. Gén. Sci. **11:** 1261. 1900; Rev. Gén. Sci. **11:** 1309. 1900; Ann. Chim. & Phys. **23:** 62. 1901.

A number of similar experiments have been performed with air, in which the motions were made visible by the introduction of smoke.[2, 3, 4] In these experiments, the layer was necessarily confined by a rigid boundary both above and below—usually a sheet of glass at the upper surface, in order to permit observation. The same phenomena of hexagonal cells and longitudinal strips or rolls were observed. Estimates of the dimensions of the cells were only approximate, but the relative dimensions appear to be much the same as in the case of liquids. The principal difference between the two cases is that the motions appear to be reversed in direction; that is, whereas in the liquid cells the upward movement occurs at the center, in the air cells it occurs at the periphery. The transition from hexagonal cells to strips, as a result of shear, occurs more readily when the shear is perpendicular than when it is parallel to a set of sides of the hexagons. The critical temperature gradient at which convection cells develop increases rapidly as the layer becomes thinner, down to a thickness of about 1 cm. Thereafter, as the layer becomes still thinner, the critical gradient becomes less again.[4]

Several theoretical treatments[5-8] of these phenomena have been given, and they are discussed in detail elsewhere in this publication.[9] All of these are based on a common point of view, originating with Lord Rayleigh. This may be stated as follows. When a system falls away from a condition of unstable equilibrium, it will do so in a preferred manner. To determine this manner, suppose that the system is subjected to a slight disturbance, characterized by a particular pattern of small displacements of the various physical quantities from their original values. Then, at any subsequent time t, each displacement may be assumed to be equal to its initial value multiplied by e^{nt}. The value of n is a function of the physical quantities involved and of the parameters characterizing the particular pattern of the disturbance, the exact functional relationship being derivable from the fundamental equations governing the behavior of the system. If n, being real, is positive, the disturbance increases, but if it is negative, the disturbance dies away.* If we consider a set of possible disturbances, then that one among them for which n is a maximum will be preferred, and the system will fall away from equilibrium in the corresponding manner. The problem of determining the behavior of the system thus reduces itself to investigating the conditions for which n is a maximum and determining that value. These conditions will involve the various physical quantities characterizing the system in its original condition and the parameters defining the pattern of the assumed type of disturbance. The limiting condition of stability will be realized when the relation between the various physical quantities is such that n is just equal to zero for the preferred disturbance, that is, when the value of n, maximized with respect to the parameters defining the disturbance, vanishes. Since the vanishing of n means that all time variations disappear, this limiting condition will represent a steady state in which the disturbance just maintains itself, as in steady convective motion. It will define a critical relation among the physical quantities involved, as well as determine the pattern of the preferred disturbance, *e.g.*, the relative dimensions of the cells in the convection problem. It should be realized that the procedure just outlined presupposes a cellular type of disturbance, and demands somewhat arbitrary assumptions as to the character of pattern, that is, as to the form of the solution of the fundamental governing equations.

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* There is, of course, the possibility that n may be imaginary or complex. This would correspond to oscillatory motion. In the type of problem under consideration, however, it can be shown that, when n is complex, the real part is negative, so that any oscillatory motion will gradually die away. (See **Pellew & Southwell.**[8])

[2] **Mal, S.** Beitr. Phys. Freien Atmosphäre **17–18:** 40–68. 1930–32.

[3] **Graham, A.** Phil. Trans. Roy. Soc. A **232:** 285. 1932.

[4] **Chandra, K.** Proc. Roy. Soc. London A **164:** 231–242. 1938.

[5] **Rayleigh, J. W. S., Lord.** Proc. Roy. Soc. London A **22:** 529. 1916.

[6] **Jeffreys, H.** Phil. Mag. **2:** 833. 1926. Proc. Roy. Soc. London A **118:** 195. 1928.

[7] **Low, A. R.** Proc. Roy. Soc. London A **125:** 180. 1929; Proc. Third International Congress for Applied Mechanics, Stockholm. 1930.

[8] **Pellew, A., & R. V. Southwell.** Proc. Roy. Soc. London A **176:** 312. 1940.

[9] **Stommel, H.** Ann. N. Y. Acad. Sci. **48** (8): 715–726.

Rayleigh, in common with all the others who have worked on the problem, assumes that the fluid is incompressible and that variations of density associated with variations of temperature are negligible, except in so far as they affect the action of gravity. In addition to this, he supposes that the two horizontal boundaries at the top and bottom of the layer are free surfaces where there is no restriction to tangential motion, although the temperature is maintained constant. Then, in the interest of mathematical simplicity, he assumes that the cells are rectangular in horizontal section. On this basis, he obtains as the condition for stability:

$$\frac{h^4\beta\gamma}{K\nu} = -\frac{27\pi^4}{4},$$

where h is the thickness of the layer, β is the thermal gradient, γ is the acceleration of gravity multiplied by the coefficient of thermal expansion, K is the coefficient of thermal diffusivity, and ν is the kinematic viscosity. He shows, also, that the preferred shape of the cell is that for which:

$$\frac{1}{L_1^2} + \frac{1}{L_2^2} = \frac{1}{8h^2},$$

where L_1 and L_2 are the lengths of the sides. It is noteworthy that the shape of the cells is independent of their thickness and of any of the other physical variables characterizing the system. Rayleigh gives, in addition, an approximate treatment of the case of hexagonal cells, but this case was first treated rigorously by Pellew and Southwell.[8]

Using the same approach as Rayleigh, Pellew and Southwell give a more general solution of the fundamental equations, without committing themselves to any particular shape of cell. They consider three different boundary conditions, in all of which the temperature is supposed to be maintained constant at the top and bottom of the layer: (a) two free surfaces, as considered by Rayleigh; (b) two rigid surfaces, at which all velocities are zero; and (c) one rigid and one free surface. For *Case a,* the limiting condition for stability is the same as that given by Rayleigh; for *Case b,* the number $27\pi^4/4$ is replaced by 1707.8; for *Case c,* it is replaced by 1100.7. It is striking that these numbers are independent of the type of cell, *i.e.,* whether square, triangular, or hexagonal. Having arrived at their general condition, Pellew and Southwell were able to derive the relative dimensions of the preferred cells for the case of hexagons as well as rectangles, and to give velocity contours within the cell. It is remarkable that, as with Rayleigh's more limited results, these dimensions were found to depend only on the boundary conditions, *i.e.,* whether free or rigid, and not at all on the thickness of the layer or the values of the various physical quantities. A summary of the numerical results is given by Stommel.

In comparing these theoretical results with the experimental findings, it will be seen that both agree that cell dimensions are independent of the values of the physical variables. In addition to this, the shape of the hexagonal cells studied by Benard, for which $L/h = 2$, L being the length of a side, is nearly the same as that calculated by Pellew and Southwell for *Case a,* where $L/h = 1.9$. It is, however, appreciably greater than that for *Case c* (where $L/h = 1.6$), which would appear to correspond more closely to the experimental conditions. Now, consider the agreement as regards the limiting conditions of stability. According to theory, for given values of the other physical variables, the critical value of the thermal gradient should be inversely proportional to the fourth power of the thickness of the layer. This has, in a general way, been confirmed by Chandra[4] in his experiments on air, for thicknesses down to about 1 cm. Below 1 cm., the law no longer seems to hold and the gradient actually increases with thickness, as already pointed out. Both theory and experiment agree, however, that in thick layers, such as those encountered in oceanography and meteorology, the critical value of the thermal gradient (or, in the case of compressible fluids, the gradient of potential temperature) should decrease very rapidly to zero, as the layer becomes thicker. In respect to the distribution of velocities, there is also general agreement between theory and experiment, as is brought out by FIGURE 1.

There are many observations pointing to the occurrence on a large scale, under natural conditions, of convective motion similar to that just discussed, both in the air and in the sea. Brunt,[10] Walker,[11] and others have pointed out the similarity of various cloud forms to the patterns observed with the aid of smoke, in a confined sheet of air, under experimental conditions. Mal[2] has explained the configurations of many upper clouds on the basis of convection cells caused by radiant heating of the lower surface and cooling of the upper surface, or by vertical displacement of nearly saturated air layers. Measurements showed that patterned cloud layers were thermally unstable, whereas uniform layers were stable. When the wind shear was low, polygonal cloud patterns prevailed, but, with high wind shear, the clouds were formed into strips. Durst,[12, 13] in a study of wind gusts, found evidence of convective circulations of a patterned nature, in the lower air over "open country." In studying clouds, he found that the distance between roll clouds lying parallel to the wind was about twice the height of the tops of the clouds, and that, with the cellular type of pattern, the diameter of the cells was about 3½ times their height. Durst[13] also examined gustiness measurements along coasts, and found some evidence of large-scale convective circulations over the sea.

An analysis, by Woodcock,[14] of soaring flight routines of herring gulls over the open ocean has revealed varying forms of ascending currents in unstable air. These currents are associated with specific thermal and flow relationships between the sea and air. In surface winds below 7 m/sec., these ascending currents appear to be columnar. In stronger winds, 7 to 13 m/sec., the rising air forms into long strips or bands, which are oriented with their long axis parallel to the wind. Thus, the changes in soaring performance of the gulls seem to indicate

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[10] **Brunt, D.** Nature **141:** 712–716. 1938.

[11] **Walker, G. J.** J. Roy. Aero. Soc. **37:** 657–680. 1933.

[12] **Durst, C. S.** The structure of wind over level country. Met. Off. Geophys. Mem. **6** (54, III): 57–63. 1932.

[13] **Durst, C. S.** Notes on the variations in the structure of winds over different surfaces. Quart. J. Met. Soc. **59:** 361. 1933.

[14] **Woodcock, A. H.** Convection and soaring over the open ocean. J. Marine Res. **3** (3): 248–253. 1940.

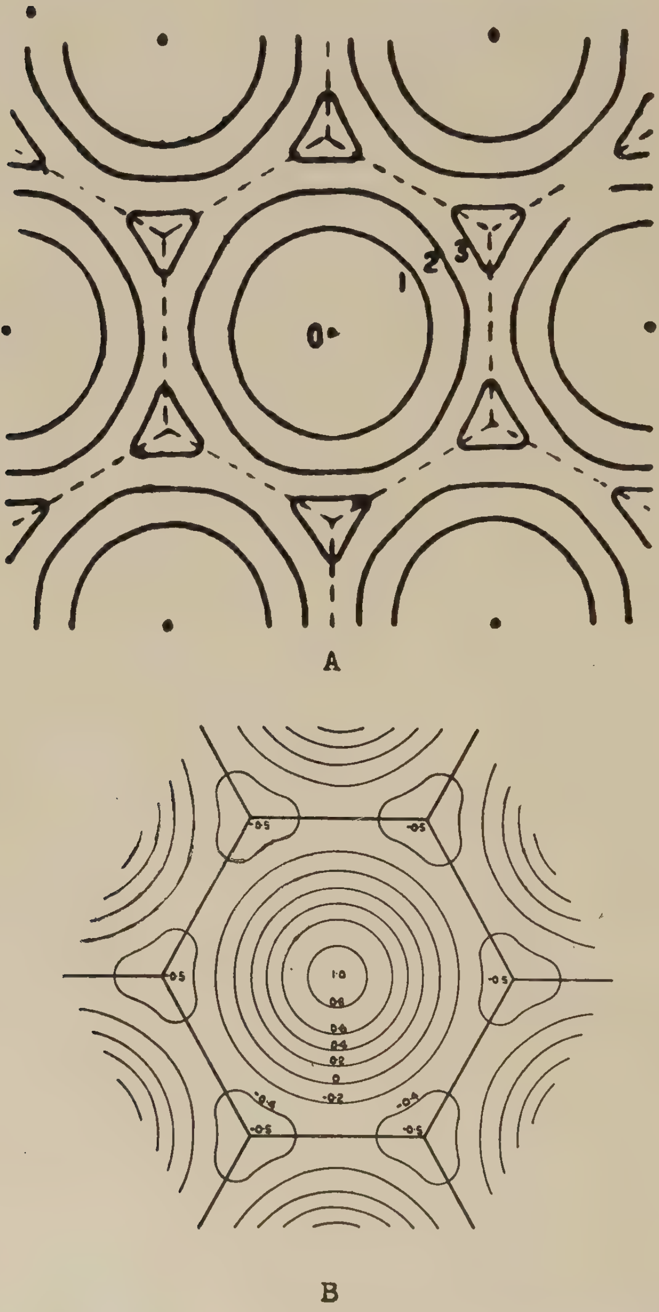

FIGURE 1. Vertical velocity contours in a horizontal plane. Upper diagram, A, shows experimental curves obtained by **Benard**[1b] for liquids. Lower diagram, B, shows theoretical curves calculated by **Pellew & Southwell.**[8]

a modification of the convective pattern from something similar to the polygonal type, at lower wind speeds, to the roll type, at higher speeds. With higher winds (>13 m/sec.), no free soaring was seen, even when the sea temperature exceeded that of the air by 10° C. This seemed to indicate that, in these cases, the vertical distribution of unstable air was taking place through random turbulent motion. When the sea surface was colder than the air, there was never any free soaring of the gulls.

The present paper gives an account of observations bearing on the problem of convective motion in the air over the sea which were made in the course of operational tests on smoke screens carried out by the United States Navy.* These tests provided an unusual opportunity to study the motion of smoke liberated on a large scale, under a variety of natural conditions. Apart from the possible effects of any heat produced by the source, the movement of smoke should represent the inherent movement of the air in which it is liberated, and the configuration which a smoke plume assumes should reflect any existing pattern of circulation in the passing air, its precise form depending on the point of release of the smoke in that pattern. The discussion which follows falls under two headings. The first deals with observations which may be interpreted in terms of the polygonal type of convection cell. It is subdivided into sections dealing with lateral and vertical displacements of the smoke. The second part deals with phenomena associated with a particular banded appearance of the sea surface observed in the Gulf of Panama, which may be explained in terms of elongated convection cells, or internal waves.

EVIDENCE FOR POLYGONAL CONVECTION CELLS

Lateral Displacement of Smoke

PLATES 1 and 2 show some interesting cases of lateral displacement in smoke released from a stationary source at sea. In PLATE 1(i), there are changes in the direction of the axis from one portion of the smoke plume to another of as much as 47°, although, within the hour prior to the production of this screen, the surface wind fluctuated by no more than 5°. Other evidence of changes in the screen axis, in the absence of significant changes of wind direction, is provided by PLATE 1 (ii), which was taken 15 minutes after PLATE 1 (i). The two plumes shown in this illustration were released 60 m. apart, the bearing between the source craft being normal to the wind. Large lateral digressions in one of the adjacent plumes showed no counterpart whatsoever in the other. If the angular digressions of the smoke from the mean downwind line were due entirely to changes in wind direction, one would expect the two plumes to be everywhere parallel. Since this was not the case, it becomes necessary to seek some other explanation for the lateral motion. If it is assumed that a system of convection cells, such as is illustrated in FIGURE 2, already existed in the air as it moved past the stationary source, then these displacements become intelligible. For instance, let us assume that the air moved so that the smoke in PLATE 1(i) was liberated along line *PQ* in FIGURE 2.* Then it is apparent that successively emitted smoke particles were subject to different displacements, depending upon where in the pattern each happened to be released. At *B*, there would be a displacement towards the convergence line *b*, at *A* an opposite displacement towards the convergence line *a*. Direct measurements of PLATE 1(i) show that the smoke at point *A* was displaced 355 feet to the left, while the air mass as a whole moved 2970 feet from the stationary source (see FIGURE 3). Similarly, smoke at point *B* was displaced 415 feet to the right, while the air mass moved 5080 feet. The proportion of lateral drift to average downwind travel is 12 per cent for point *A* and 8.2 per cent for point *B*. Since the mean surface wind speed was 9 knots or 4.6 m/sec., this means that the speed of lateral motion in this portion of the convective system was about 0.52 m/sec. This relatively small lateral motion would produce only about a 5° change in wind direction at the smoke source, yet the assumed pattern of convection would account for angular deviations of the smoke plume from its average direction up to 60°. Thus, the assumption of some such convective system as that shown in FIGURE 2 may be used to explain how large lateral displacements of a screen axis can occur when there is only a slight change in wind direction. It is not to be supposed, however, that the perfect geometrical regularity shown in FIGURE 2 will ever be completely realized in the free air over the sea.

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* Except when otherwise indicated, the smoke used in tests described in this paper was oil fog.

PLATE 3A shows smoke laid crosswind by a vessel which also dropped a line of floating pots as she proceeded. The main smoke screen is aligned with the apparent wind on the vessel. The smoke from the stationary pots lies along the true wind. It will be seen that the plumes from the pots show lateral displacements which point towards regions of ascent, as revealed by towers in the crosswind screen. When

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* In model experiments (cf. **Graham**, 287[3]), the orientation of the cell system in respect to the direction of shear has been found to be sometimes parallel with OX, sometimes parallel with OY (FIGURE 2). Alignment with OX is associated with lower rates of shear, and alignment with OY with higher rates of shear. Intermediate orientations might also be expected.

PLATE 3A is traced upon a photogrammetric grid of proper size and perspective, as in PLATE 3B, the effect becomes more apparent. Large displacements to either side of the mean direction of the true wind can be seen. Also, it can be verified that the displacement, in every case, is towards one of the rising towers in the main crosswind screen. The average spacing between these towers is 1300 feet.

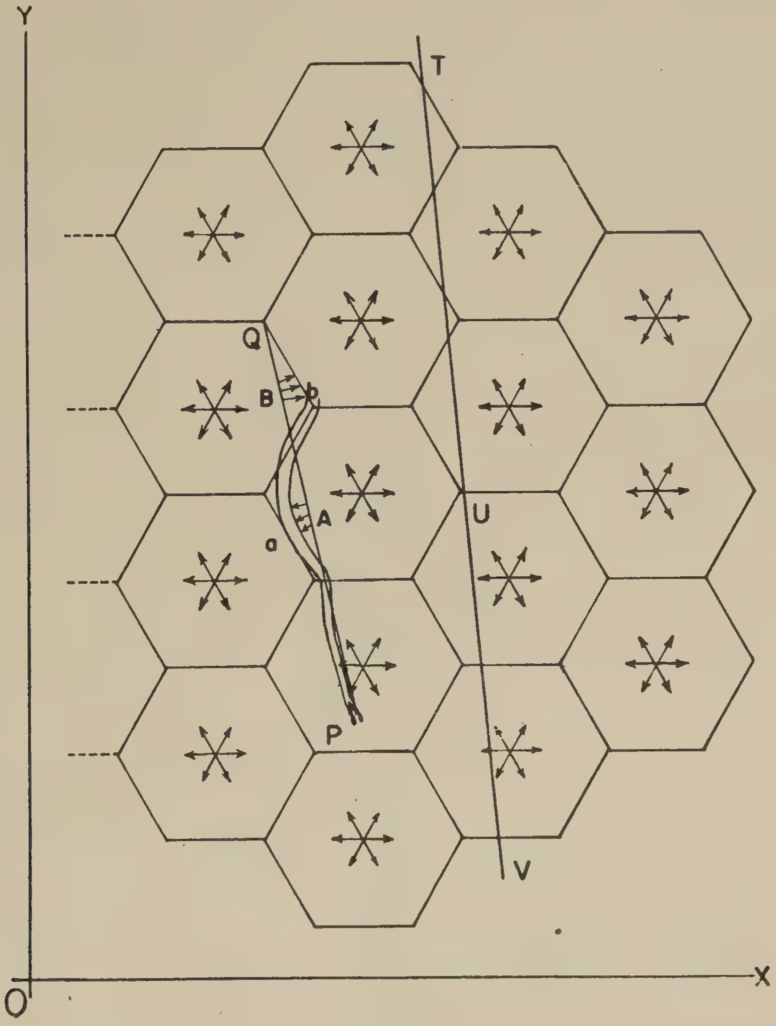

FIGURE 2. Diagram illustrating steady-state hexagonal convection cells, with descending air at the cell centers and ascent on the periphery.

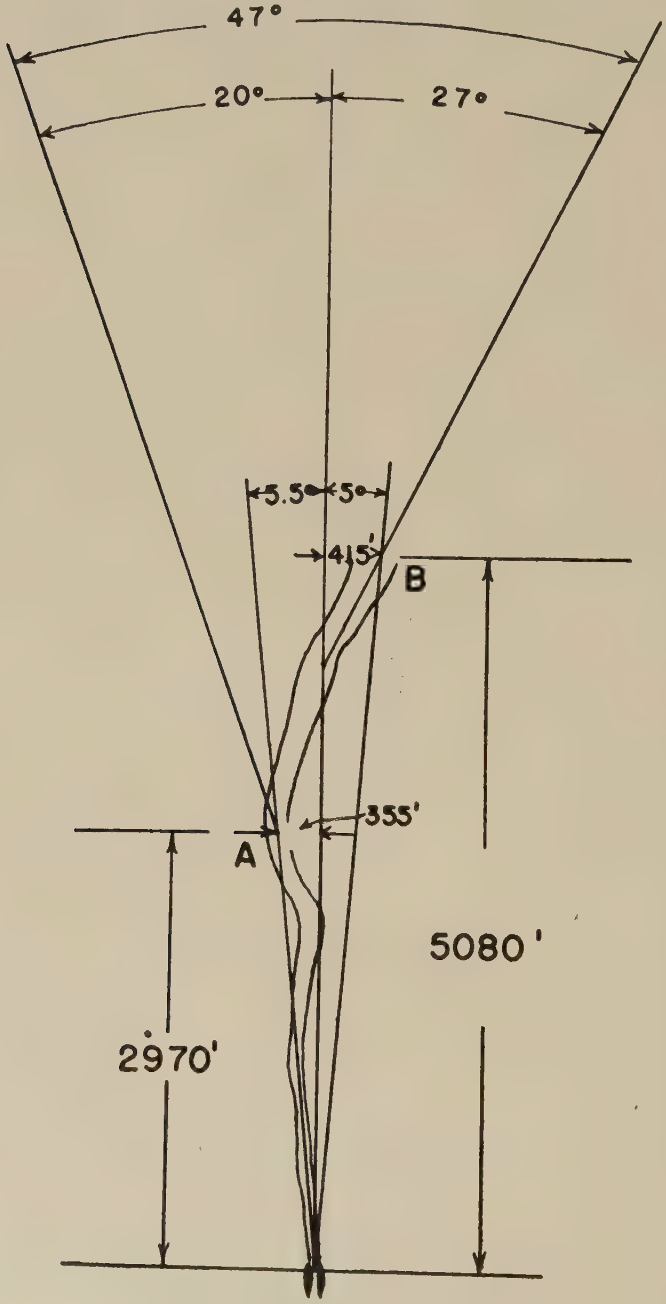

FIGURE 3. Plan of smoke screen shown on PLATE 1(i).

Vertical Displacement of Smoke

Examples of vertical displacement of smoke are shown in PLATE 4. These photographs were taken within a few minutes of one another, in such a brief interval that there was practically no change in the meteorological conditions. The very great difference in the appearance of successive portions of the smoke shown in different pictures is attributed to the continuously changing position of the moving source, relative to the convective circulation pattern in the passing air. If the source were located so that the smoke were liberated along the segment *TU* in FIGURE 2, the spacing and the character of the ascending and descending regions should be quite different from what they would be if the source were so located as to produce smoke along *UV*. It is suggested that the portion of the screen shown in PLATE 3B may correspond to some such segment as *UV* in FIGURE 2, and the portions shown in PLATE 4, (i) and (ii), to some such segment as *TU*, the pattern having meanwhile changed position in relation to the source. In addition to this, the inevitable irregularities of the prevailing pattern of convection will have their counterpart in the movement of the smoke. It will be noticed that there are about twice as many ascending zones in PLATE 4(iii) as in PLATE 4(i). The situation may be further complicated by a tendency, pointed out by Benard, for the vertical motion to be accentuated at the vertices of the hexagons (see FIGURE 1). It will be seen that the relations of segments *TU* and *UV* to the vertices are quite different. Thus, the assumption of a polygonal convection pattern may be used to explain the rapid change in the spacing of the regions of ascent, in PLATE 4 (i–iii).

Other illustrations of the vertical displacement of smoke are provided by PLATE 5. These show chemical smoke (FS) laid by a plane flying a horizontal course directly to windward at a speed of 120 knots and an altitude of 300 feet. The initially straight plume became progressively distorted into vertical loops, some portions of the smoke being ultimately carried down to the surface, while other portions suffered a corresponding rise. While this occurred, the mean height of the plume axis remained essentially unaltered. Measurements of a series of timed photographs not contained in this paper indicate vertical velocities of the order of 3 feet per second. At about this time, observations showed that the air was almost exactly adiabatic up to 1200 feet (the limit of height of the measurements). The surface water was 0.2° C. warmer than the air at deck level.

EVIDENCE FOR LONGITUDINAL ROLL VORTICES

Plates 6–8, which were taken at 700 feet, show a peculiar banded appearance of the sea surface commonly observed in the Gulf of Panama. The effect seems to be due to a systematic variation in the pattern of small waves on the sea surface, associated with a corresponding variation in wind speed. At first glance, the appearance might have been ascribed to a long swell, but further consideration showed that this was not the explanation, for no swell was present, as confirmed by reports from surface ships, and the bands sometimes stopped abruptly, far from shore. Moreover, they did not move with the speed requisite for long waves.

Table 1

Gulf of Panama

Date	Roger time*	Air T °C.	Sea T °C.	Wind speed knots	Wind direction	Cloudiness		Sea T-Air T °C.
						%	Type	
Jan. 28	1345	26.40	25.70	5	260°	9	Ci	−.70
28	1435	26.50	26.20	5	295	10	Ci	−.30
28	1530	26.60	26.05	13	330	10	Ci	−.55
28	1605	26.05	25.80	13	325	10	Ci	−.25
Jan. 29	1410	26.95	26.70	4	55	5	Ci str	−.25
29	1525	26.78	26.20	7	—	10	Ci str	−.58
29	1635	26.80	26.30	12	35	8	Ci str	−.50
Jan. 30	1410	27.20	26.45	9	25	10	Ci cu Ci str	−.75
30	1540	26.95	26.50	5	35	9	Ci cu Ci str	−.45
30	1745	27.60	26.80	2	—	10	Ci cu Ci str	−.80
Jan. 31	1420	27.05	26.55	9	25	4	Ci str	−.50
31	1540	27.45	26.50	9	30	6	Ci str	−.95
31	1635	27.55	26.50	15	30	4	Ci str	−1.05
Feb. 5	1320	26.20	26.00	5	270	Clear		−.20
5	1400	26.20	26.20	0–3	270	Clear		0.0
5	1530	26.70	26.80	0–3	300	Clear		.10
Feb. 6	1400	26.40	25.70	10	50	Clear		−.70
6	1525	26.90	26.05	Calm	—	Clear		−.85
6	1650	27.20	26.30	1–7	000	Clear		−.90

* = 4 hours behind Greenwich mean time.

Table 1 shows the general meteorological conditions on a number of days when the bands were observed, and figures 4, 5, and 6 show air thermograph traces giving the temperature gradient in the lower air. With one exception, these are all of the same general type. All these

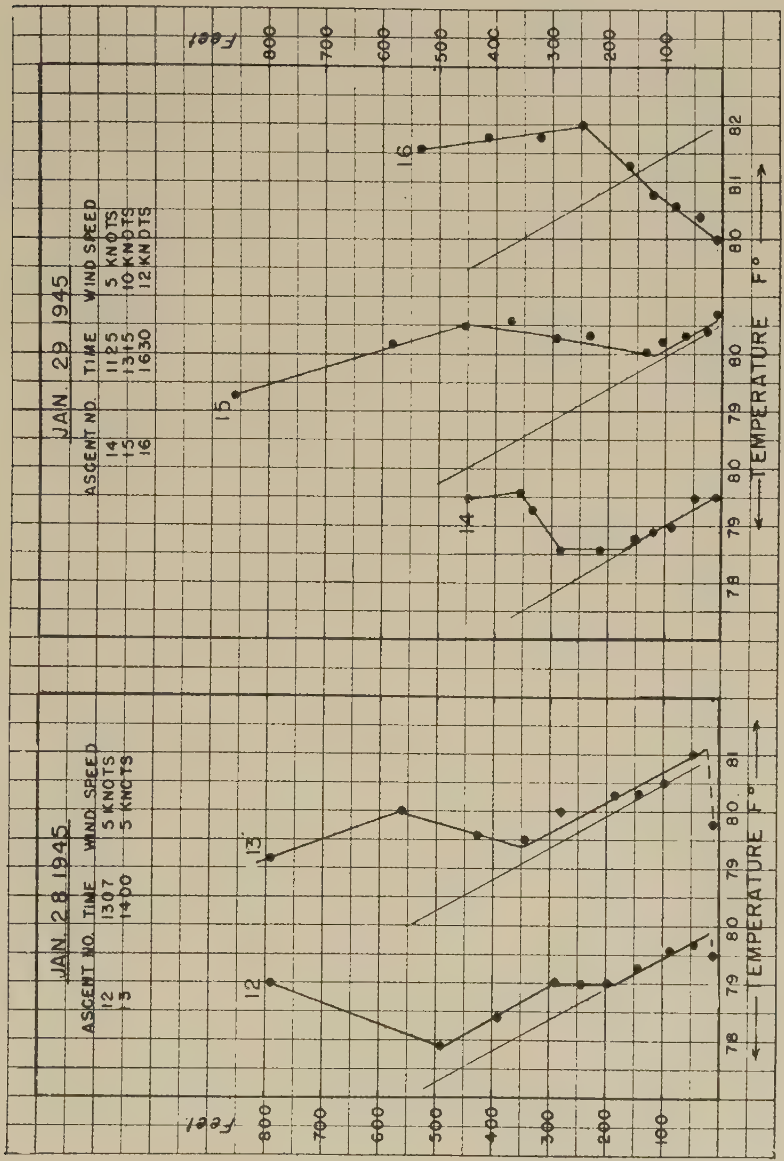

FIGURE 4. Temperature lapse rates during periods when the bands were visible on the sea surface.

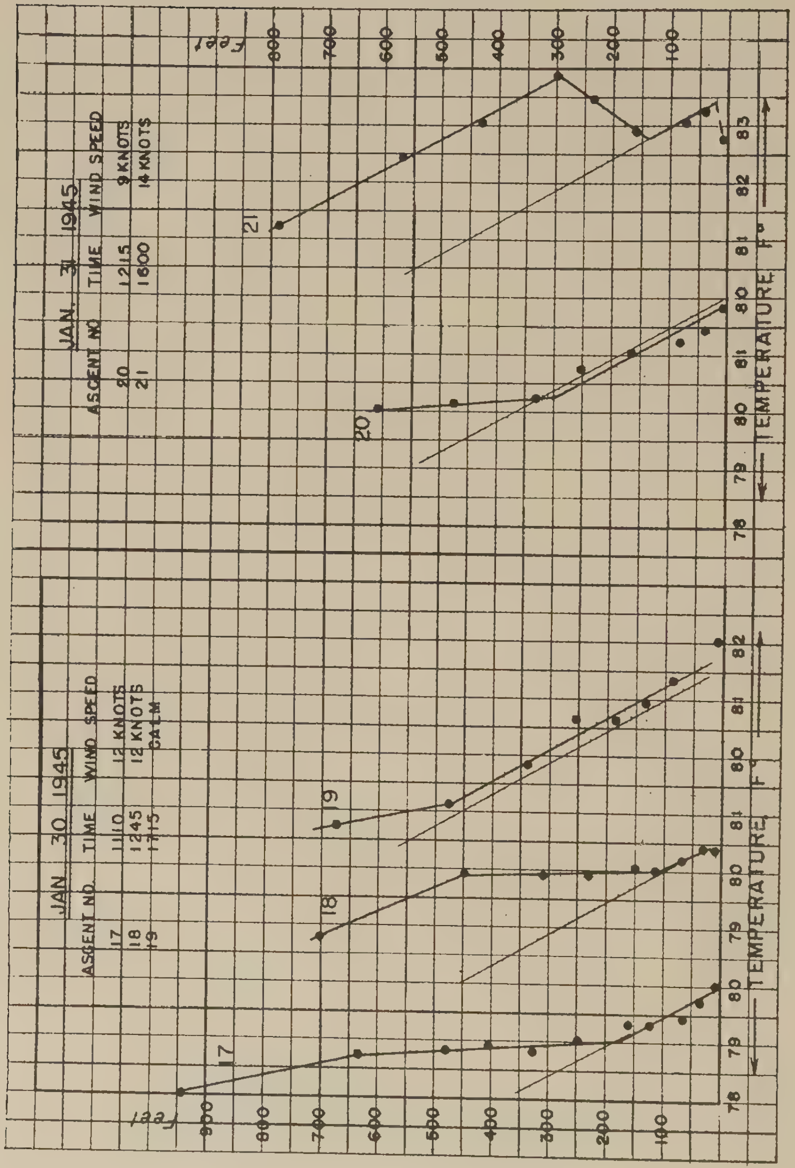

FIGURE 5. Temperature lapse rates during periods when the bands were visible on the sea surface.

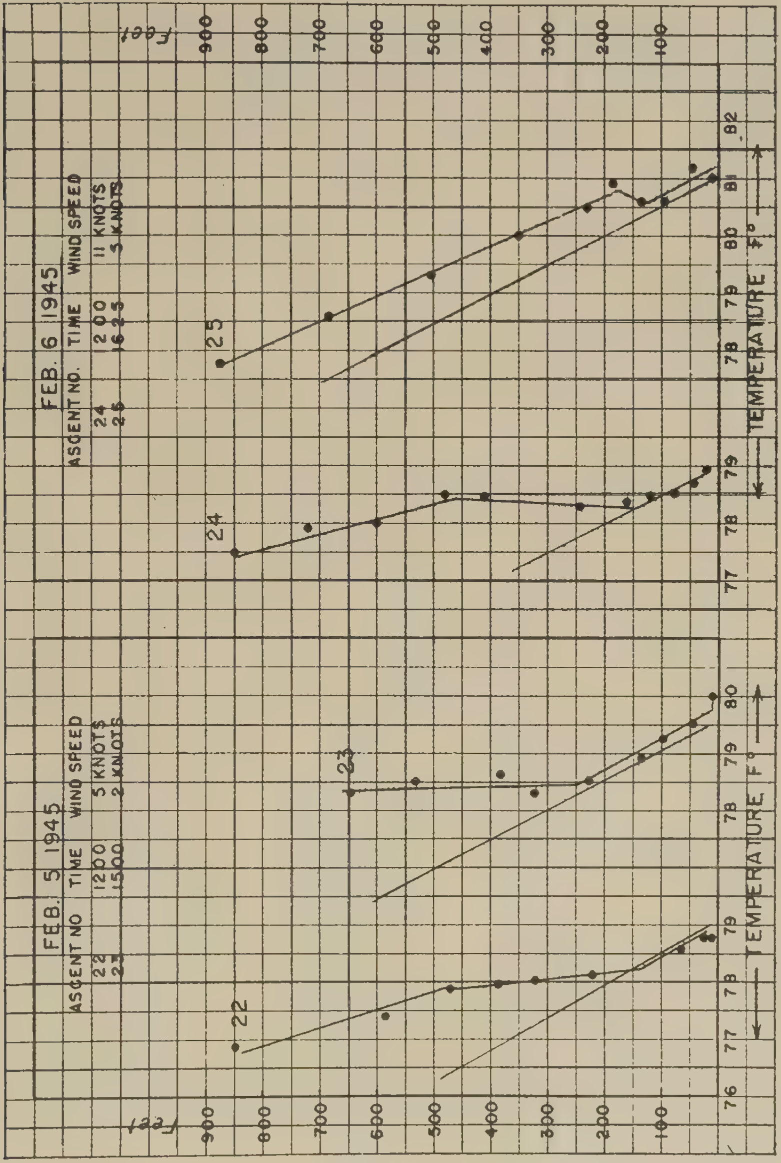

FIGURE 6. Temperature lapse rates during periods when the bands were visible on the sea surface.

days were characterized by the presence of a surface layer of relatively well mixed (adiabatic) air rather sharply separated from an overlying layer of stable air at a height of several hundred feet. Between the two layers, there was a large change in wind speed and often also in wind direction, made evident by the movement of the smoke (PLATE 9). The directional relationships between the upper and lower winds and the bands, determined photogrammetrically on the basis of smoke distribution, are shown in FIGURE 7.* In general, it may be stated that, whenever bands occurred, surface winds were moderate, the lower air was mixed, the upper air was stable, the sun was high, and there was no heavy cloud cover. The long axis of the bands was oriented roughly in the direction of the apparent wind in the upper layer, with reference to the moving air below.

On the basis of these considerations, it is tentatively concluded that the bands are due to the presence either of a system of longitudinal roll vortices, somewhat as shown in FIGURE 8, or to a system of internal waves in the mixed surface layer. Either explanation would account for the regular variation of wind over the surface indicated by the bands. The hypothesis of roll vortices is consistent with the observed orientation of the bands, for Mal,[2] Graham,[3] Chandra,[4] and others have found that paired vortices are usually formed with their long axes parallel with the shear. The shear at the upper boundary of the surface layer has the same direction as the apparent wind in the upper layer with reference to the moving air below. In order to visualize it, let us imagine a ship moving with the speed, and in the direction, of the air at the surface, and having a mast high enough to penetrate the upper layer. A flag on this mast will indicate the apparent wind aloft with reference to the surface wind and will thus show the direction of the shear between the two layers. It is not to be overlooked that the shear between the lower wind and the sea surface will also be involved in determining the orientation of the vortices, so that, ideally, we might expect some deviation of the bands from the direction just discussed towards that of the surface wind itself.

There are two other phenomena associated with the bands which deserve consideration: (1) the configuration of a smoke plume laid at right angles to the bands; and (2) the relationship of the band spacing to the height of the adiabatic layer and to the width of the smoke cells.

1. PLATES 7 and 8 show the performance of a smoke screen laid at right angles to the bands. The surface convergence of the smoke,

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* Unfortunately, no wind speed measurements aloft were made. In FIGURE 7, the length of the arrows is not to be taken as representing relative wind speeds.

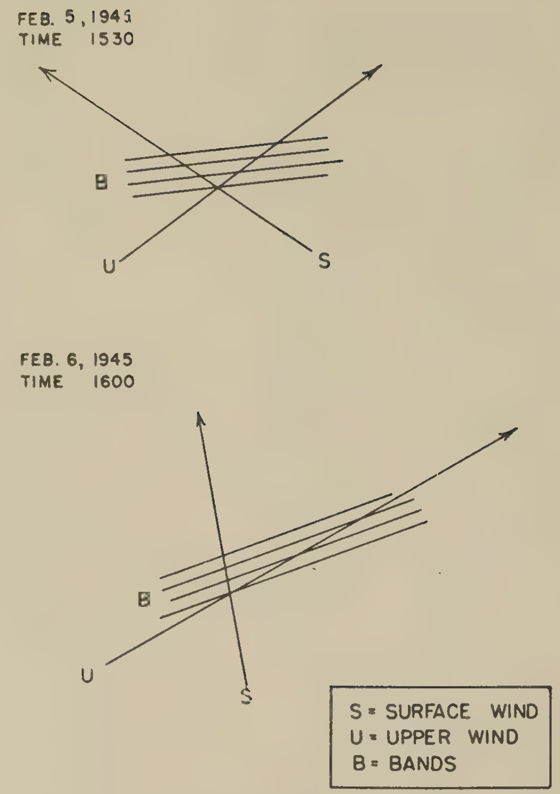

FIGURE 7. Approximate orientation of bands relative to surface and upper wind directions as determined photogrammetrically.

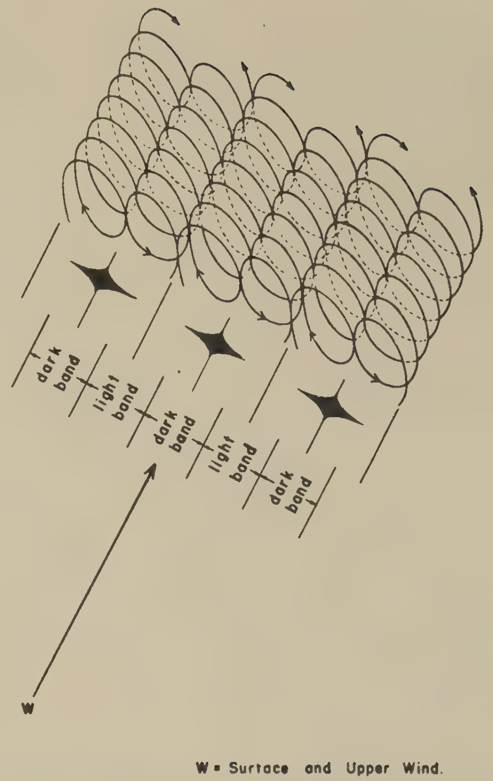

FIGURE 8. Diagram of hypothetical roll vortices. Shaded areas represent darkening of sea surface where faster moving upper air is brought down into contact with the sea surface.

its rise, and its divergence at the top of the mixed layer are visible at point *D*. The growth of a subsequent convergent tower of smoke can be followed at point *E* (the average rate of rise at point *E* being 3 ft/sec., as determined photogrammetrically from successive pictures). At point *F*, in PLATES 7 and 8, the progressive descent of smoke in an eddy may be followed. These figures illustrate the presence of ascending and descending air motion in the banded areas.

2. The average distance between the bands, in PLATE 7(i), is about 1000 feet. At this time, the average distance between the convergence points, *D* and *E*, in PLATES 7(ii) and 8(i), was 950 feet. The height of the mixed (adiabatic) layer of air was 480 feet [PLATE 5(ii), ascent No. 19]. Thus, it seems that the width of the bands is about the same as the width of the smoke cloud formations and about twice the height of the mixed layer. This is in agreement with what would be expected on theoretical grounds for roll vortices (see figures given by Stommel). The average height of the smoke cloud formations (560 ft.) is somewhat greater than that of the mixed layer (480 ft.). This may be caused by the penetration of the smoke into the stable layer above, due to associated heat, or it may be due to a variation in the height of the layer with time.

In the last two paragraphs, we have stressed the interpretation of the bands in terms of roll vortices. An alternative explanation in terms of a system of internal waves should not be overlooked. Such waves would have their origin in the purely mechanical effect of shear at the top and bottom of the mixed layer, and would not demand a condition of thermal instability. Actually, on most of the days when the bands were observed, the sea surface was colder than the air, as will be seen from TABLE 1. In contrast to internal waves, roll vortices, originating in thermal instability, would appear to demand that the sea be warmer than the air. Thus, Brunt[15] says, "Frictional forces have little or nothing to do with the genesis of the circulation, which in fact dies away rapidly through the action of friction as soon as the transfer of heat dies away." Brunt refers here to observations on experimental model systems, but he implies that the same would be true in free air. It should not be overlooked, however, that the water temperatures given in TABLE 1 are based on dip bucket samples. It is possible that these may not give a true picture of the real surface temperature. In the absence of adequate mixing by the wind, the surface might develop an excess of temperature in relation to the air and the underlying water. This would escape detection by the dip bucket technique, and there might be an unsuspected flow of heat from the water to the air. The moderate surface winds and relatively slight cloudiness (only thin cirrus clouds were present) which obtained on most of the days when the bands were observed suggest that this might have been the case. It is also possible that greater humidity of the air close to the surface, due to evaporation, may have contributed significantly to produce instability, since, of course, moist air is lighter than dry air. No precise data bearing on the point were obtained, but it should be noted that, at 80°, a 10 per cent change of relative humidity has an effect on density equal to a .7° F. change of temperature. In the absence of further information, any final decision between an explanation in terms of roll vortices and one in terms of internal waves must be left open.

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[15] **Brunt, D.** Physical and Dynamical Meteorology: 219–223. Columbia University Press (2nd edition). London. 1939.

DISCUSSION OF THE PAPER

Professor B. Haurwitz:

In connection with the observations of polygonal cells, it is relevant to refer to a paper by H. Solberg* in which, among other problems, cellular oscillations in an atmosphere with a linear lapse rate are considered. For a cell whose dimensions resemble that of the Benard cell and for a temperature lapse rate of 6° C. per 1000 m., the period of the oscillation is found to be 13 minutes. It would be interesting to know if any such periods have been observed in connection with the convection patterns. If such periods happen to be very similar to those computed by Solberg, it would tend to show that the patterns set up by convection conform to the free oscillations of the atmosphere.

A theoretical treatment of the cloud rolls as convection patterns is still lacking. It would be desirable especially in order to see in which cases such a theory gives the correct spacing of the cloud rolls and in which cases the theory of internal waves gives better results, or if both theories lead to the same spacing of the patterns.

As far as the laboratory experiments on convection patterns are concerned, it is surprising that, while in liquid cells the ascending motion takes place at the center, in air cells it does so on the periphery. It would be interesting to know if any explanation for this difference can be given. Theoretically, both types of motion would appear to be equivalent, the direction of motion only depending on whether a certain constant is positive or negative.

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* Astrophysica Norvegica 2(2). 1936.

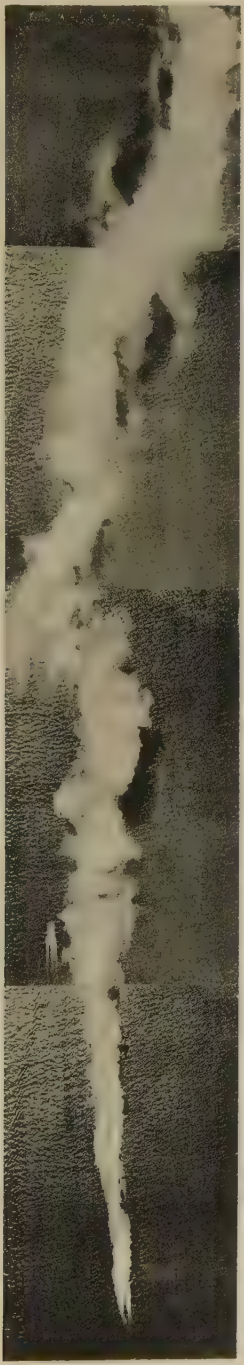
PLATE 1

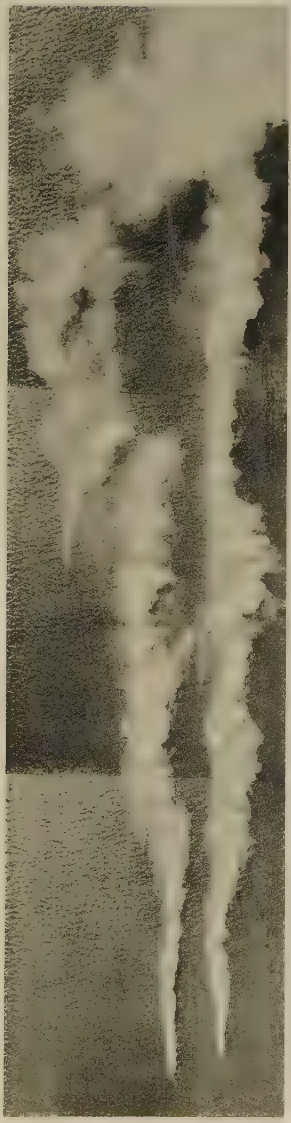
(i) Vertical view of smoke from a stationary source, showing the lateral displacement to the right and left of the mean line of travel.

June 14, 1944.
Time: 1610.
Wind: 4.6 m/sec.
Length of smoke plume: 1545 m.

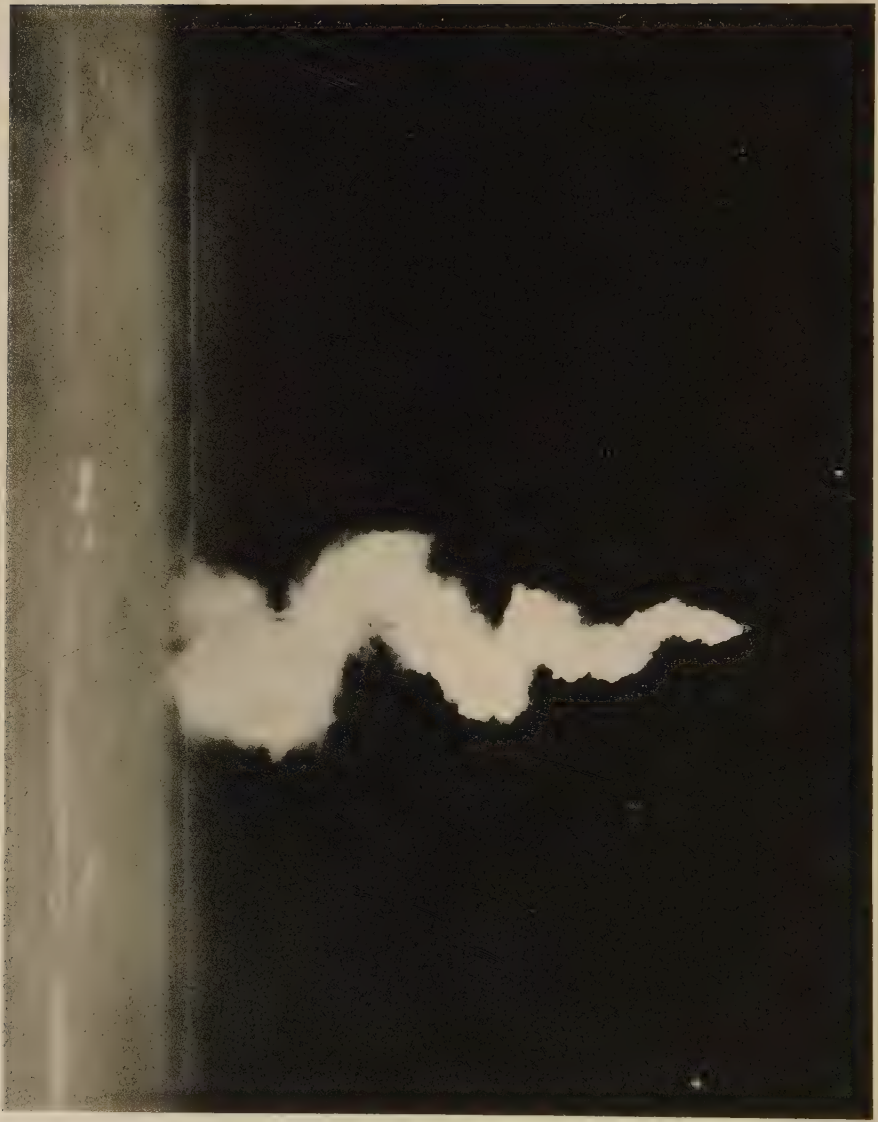
Sea Surface T.: 29.1° C.
Air T. at 3 m.: 28.1° C.
Fetch: > 100 nautical miles.

(ii) Vertical view of smoke from two sources about 60 m. apart. Date and conditions same as for (i), but time 15 minutes later. Note markedly different lateral displacement of the two smoke plumes. Length of plumes: 1230 m.


(i)


(ii)

WOODCOCK AND WYMAN: CONVECTION OVER THE SEA



WOODCOCK AND WYMAN: CONVECTION OVER THE SEA

PLATE 2

Oblique view of smoke from a stationary source, showing the lateral displacement to the right and left of the average wind direction.

August 29, 1944.
Time: 1100.
Fetch: 20 nautical miles.
Wind: 7.7 m/sec.

Sea Surface T.: 21.0° C.
Air T. at 3 m.: 19.8° C.

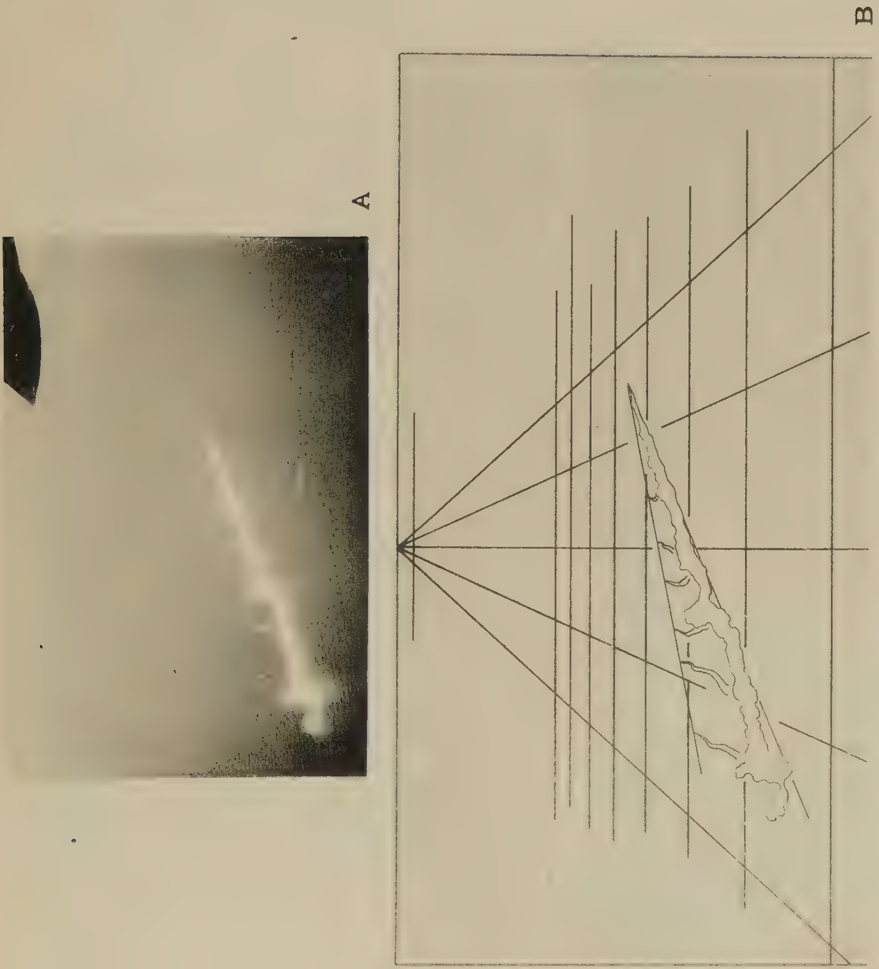
Plate 3

A. Oblique view of smoke laid crosswind by a vessel which also dropped a line of floating smoke pots. Note the lateral displacement of the smoke from the floats toward the high points in the transverse screen.

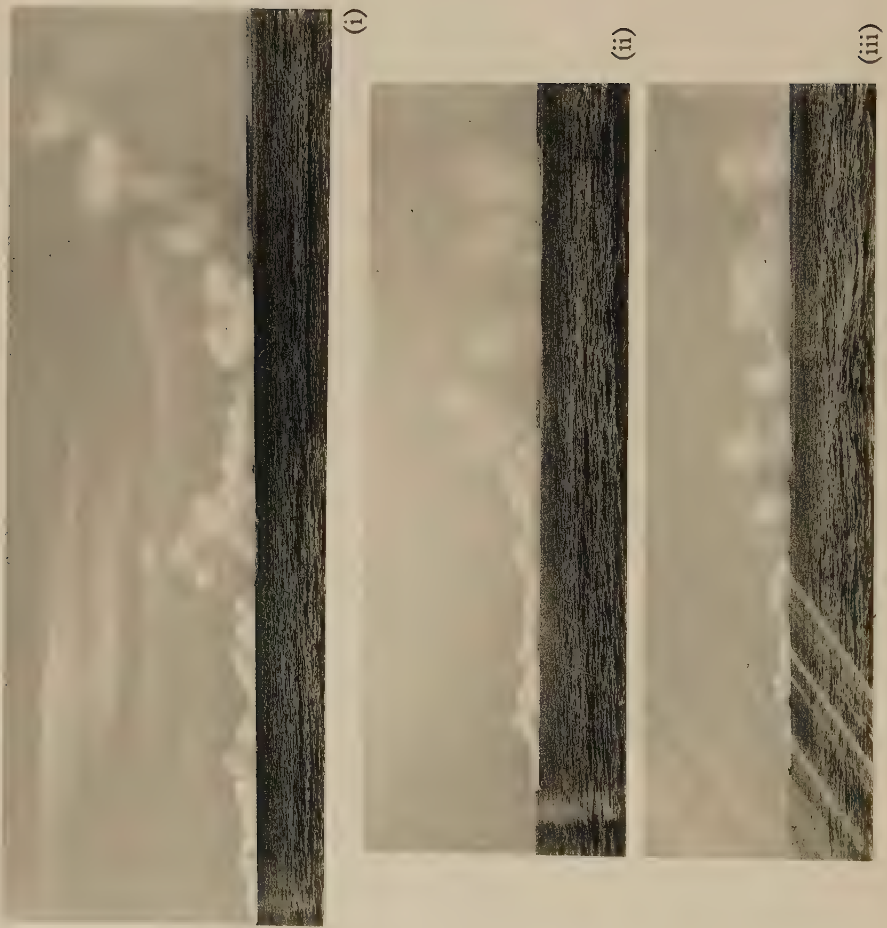
December 12, 1944.
Time: 1100.
Fetch: 500 nautical miles.

Wind: 6.5 m/sec.
Sea Surface T.: 26.5° C.
Air T. at 12 m.: 25.7° C.

B. Outline of smoke shown in A upon a scaled photogrammetric grid. Note the large divergence of the float smoke from the parallels. Distance between grid lines: 2250 ft.



WOODCOCK AND WYMAN: CONVECTION OVER THE SEA



WOODCOCK AND WYMAN: CONVECTION OVER THE SEA

PLATE 4

(i) Surface view of smoke laid by craft moving 6.5 knots to windward. Note the widely-spaced vertical smoke developments.

August 7, 1943.
Time: 1040.
Fetch: 20 nautical miles.

Wind: 2.2 m/sec.
Sea Surface T.: 22.3° C.
Air T. at 3 m.: 18.4° C.

(ii) Date and conditions same as for (i), but time 10 minutes later. Note partitioning of the smoke.

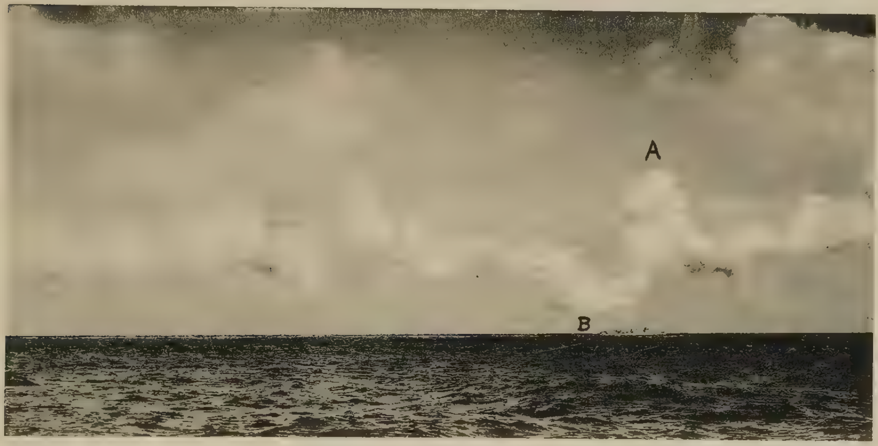
(iii) Date and conditions same as for (i) and (ii), but time 20 minutes later than in (i). The spacing of regions of ascent is about one-half that shown in (i).

PLATE 5

Smoke laid parallel to the wind by a plane flying horizontally. Note the vertical development of points A and B. Elapsed time between (i) and (ii) is 88 seconds.

December 19, 1944.	Wind at 10 m.: 6.2 m/sec.
Time: 0945.	Sea Surface T.: 26.3° C.
Fetch: > 500 nautical miles.	Air T. at 10 m.: 26.1° C.
Altitude of plane: 92 meters.	
Air speed of plane: 120 knots.	

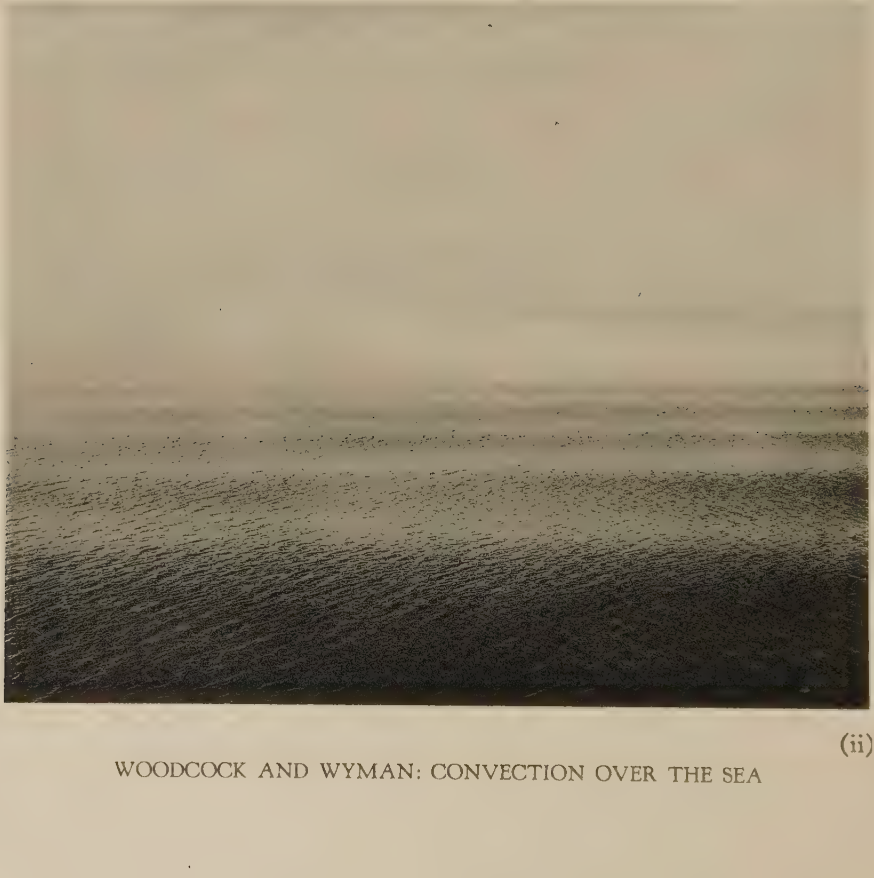
(i)



(ii)

WOODCOCK AND WYMAN: CONVECTION OVER THE SEA

(i)



(ii)

WOODCOCK AND WYMAN: CONVECTION OVER THE SEA

PLATE 6

(i) Oblique view showing dark and light bands on sea surface lying parallel to the surface wind.

January 30, 1945.
Time: 1355.
Fetch: 37 nautical miles.

Wind: 4.5 m/sec.
Sea Surface T.: 26.4° C.
Air T. at 12 m.: 27.2° C. ci. st.
Clouds: 10 ci. cu.

(ii) Oblique view showing dark and light bands on sea surface lying parallel to the surface wind.

January 30, 1945.
Time: 1510.
Fetch: 37 nautical miles.

Wind: 3.9 m/sec.
Sea Surface T.: 26.5° C.
Air T. at 12 m.: 26.9° C. ci. cu.
Clouds: 9 ci. st.

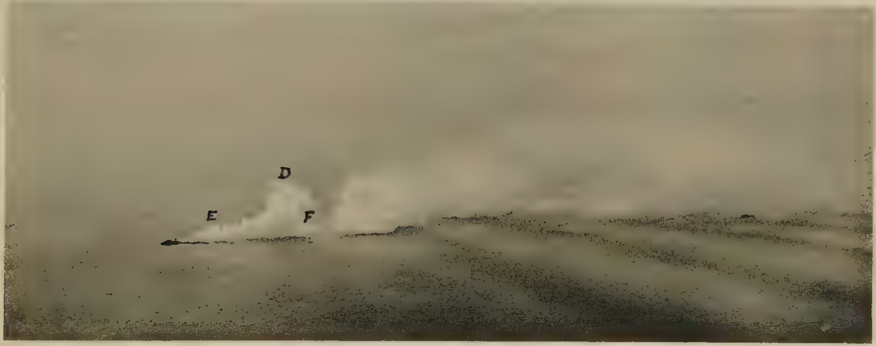
Plate 7

(i) Oblique view of smoke laid across the bands in such a manner as to show the motion of the overlying air. Plates 7 (i) through 8 (iv) were taken in quick succession on January 30, 1945.

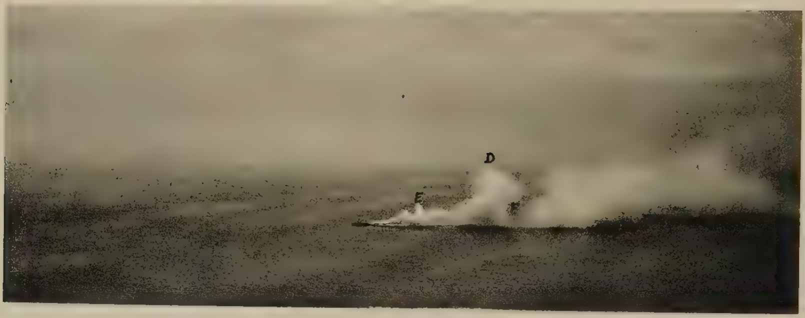
Time: 1630:25.	Sea Surface T.: 26.7° C.
Fetch: 33 nautical miles.	Air T. at 12 m.: 27.3° C.
Wind: 1.5 m/sec.	Clouds: 9 alt. cu.

(ii) Date and conditions same as for (i), but time 3 minutes 15 seconds later. Note the progressive development at points d and e in plates 7 (ii) through 8 (iv).

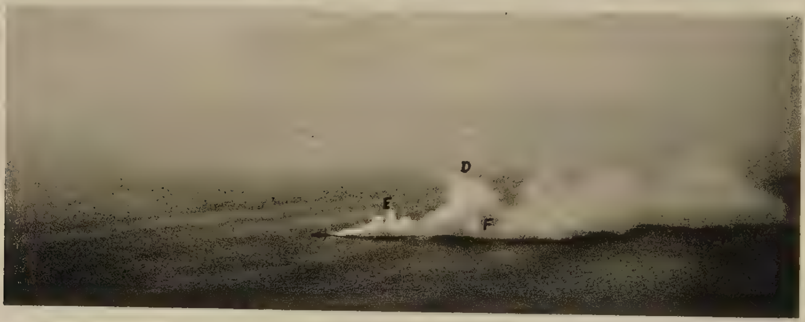
(i)



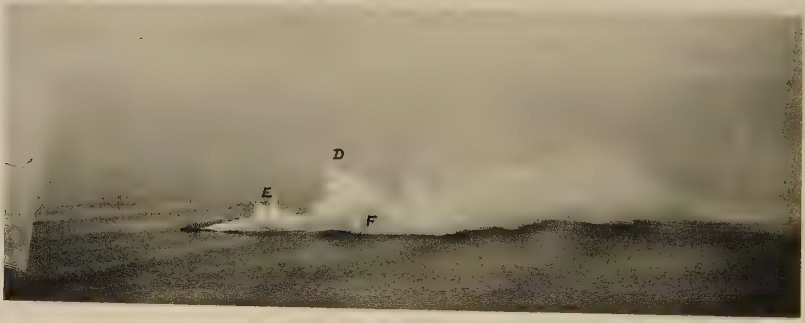
(ii)



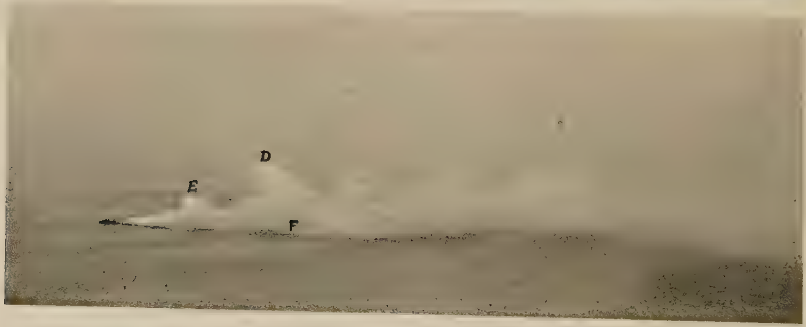
(i)



(ii)



(iii)



(iv)

WOODCOCK AND WYMAN: CONVECTION OVER THE SEA

PLATE 8

(i) Date and conditions same as for PLATES 7 (i) and (ii), but time 3 minutes 37 seconds later than in PLATE 7 (i).

(ii) Date and conditions same as for PLATES 7 (i) and (ii) and PLATE 8 (i), but time 3 minutes 49 seconds later than in PLATE 7 (i).

(iii) Date and conditions same as for PLATES 7 (i) through 8 (ii), but time 4 minutes 1 second later than in PLATE 7 (i).

(iv) Date and conditions same as for PLATES 7 (i) through 8 (iii), but time 4 minutes 11 seconds later than in PLATE 7 (i).

PLATE 9

Vertical view of smoke, showing large change in wind direction within the first few hundred feet of the sea surface.

February 5, 1945.	Wind at 6 m.: 1m/sec.
Time: 1530.	Sea Surface T.: 26.8° C.
Fetch: 26 nautical miles.	Air T. at 12 m.: 26.6° C.
	Clouds: none.

WOODCOCK AND WYMAN: CONVECTION OVER THE SEA

Contribution No. 357

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INTRODUCTION: PROBLEMS CONCERNING CONVECTIVE LAYERS

By R. B. Montgomery

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The first conference of the Section of Oceanography and Meteorology of The New York Academy of Sciences, in March, 1942,† concerned the subject of boundary-layer problems. It so happened that most of the problems discussed were ones which are controlled by mechanical turbulence. The second conference (of which this publication is the result) deals with convection patterns and related phenomena in horizontal layers, and might have been entitled *Convective-Layer Problems.* Since convective layers usually coincide with boundary layers, this subject supplements that of the first conference. This second publication, moreover, is concerned with boundary layers which are controlled by convection, either convection of an orderly, patterned type, or convection of the irregular type known as thermal turbulence.

By *convective layer* is meant a layer in which, due to unstable hydrostatic equilibrium, the potential energy of the vertical mass distribution is converted into thermal turbulence or patterned convection. This use of the word "convection" is the restricted one customary in meteorology. In order that the full implication of individual studies may be seen, the various convective layers in the ocean and atmosphere may profitably each be mentioned.

(1) *Nocturnal type of surface layer in water* (FIGURE 1). The lower limit of this convective layer can be a thermocline, or it can be the bottom of the body of water. The convection is maintained by surface cooling due to long-wave radiation, by heat conduction to the atmosphere, and by loss of latent heat in evaporation. In salt water, evaporation produces a salinity gradient which contributes to the convection.

(2) *Insolational type of surface layer in water* (FIGURE 2). Even though the heating effect of short-wave, solar radiation may exceed in total magnitude the factors, mentioned above, which increase the water

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* Contribution No. 357.
† Ann. N. Y. Acad. Sci. **XLIV** (1): 1–104. 1943.

density, a shallow surface layer often exists in which those factors predominate. This is true because the short-wave radiation is absorbed throughout several meters of water, while the emission of long-wave radiation and the direct effects of evaporation are confined to a surface film about one millimeter thick.

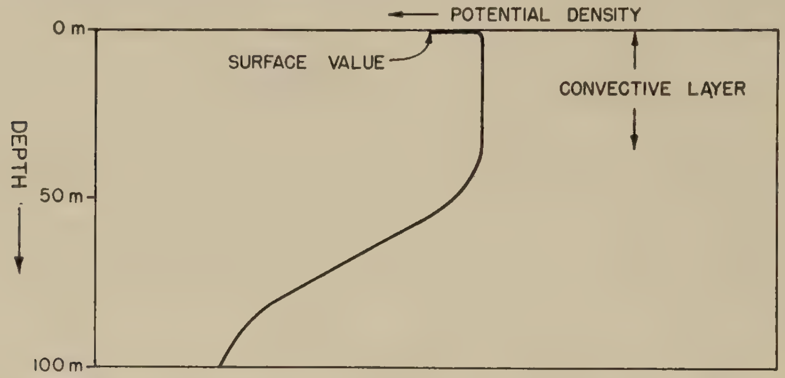

FIGURE 1. Schematic representation of nocturnal type of surface convective layer in water.

(3) *Air layer warmed at surface* (FIGURE 3). A convective air layer capped by a temperature inversion, or stable layer, can be formed by matutinal warming of the ground under it, or by the advection of the air to a warm water surface. The potential temperature of the convective layer steadily increases.

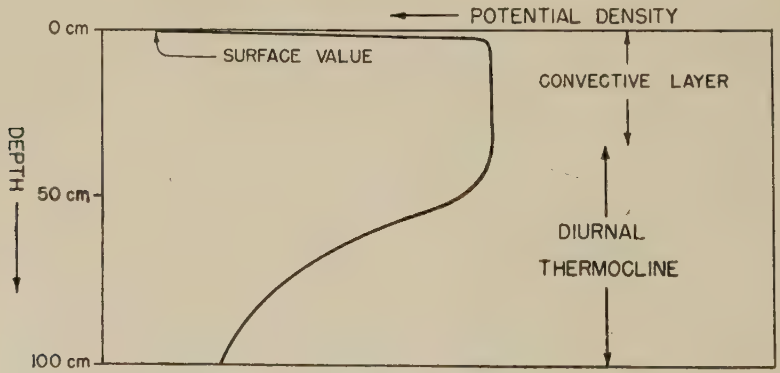

FIGURE 2. Schematic representation of insolational type of surface convective layer in water.

(4) *Air layer cooled from above* (FIGURE 4). The top of a cloud sheet or fog loses heat by radiation at a large rate, if there are no clouds above it, perhaps even in the presence of strong insolation. A convective layer developing in this way may, or may not, extend to the ground. Its potential temperature steadily decreases.

(5) *Air layer warmed from below and cooled from above.* The cloud layer shown in FIGURE 4 may be so high that it is much colder than the ground. Its base then gains heat by long-wave radiation from the ground. The resulting convective layer may be confined to the cloud layer. While warming by radiation from below occurs when the actual temperature of the cloud base is lower than the surface temperature, warming by convection from the ground occurs when the potential temperature of the cloud base is lower than the surface temperature (FIGURE 5). The convective layer, in this case, extends from the top of the cloud down to the surface. Fog may form a special case of this phenomenon. When warming from below and cooling from above occur simultaneously, the relative effectiveness of the two determines, of course, whether the temperature of the convective layer increases or decreases.

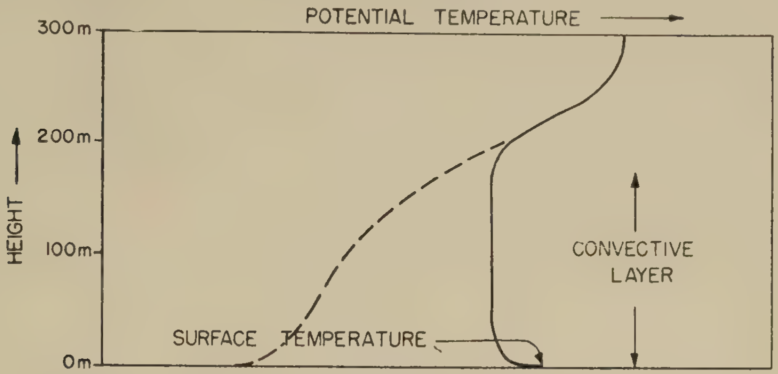

FIGURE 3. Schematic representation of convective air layer warmed at surface.

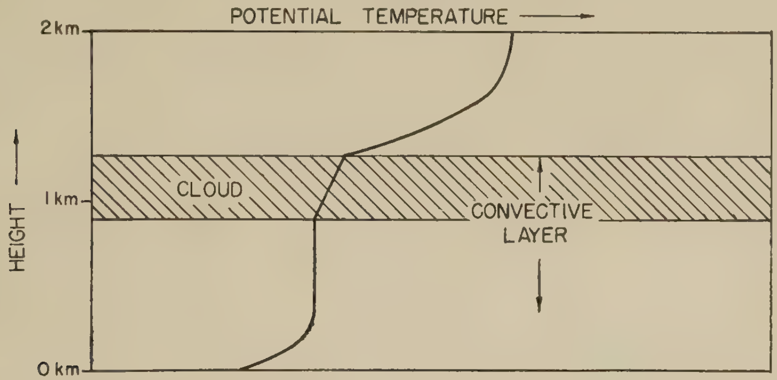

FIGURE 4. Schematic representation of convective air layer cooled at cloud top, with saturated-adiabatic lapse rate in cloud.

In its pure form, each of these five types of layers is horizontally uniform, except for the natural convection pattern belonging to it. In order to confine the subject within reasonable limits, the forced patterns resulting from topographic features or from explosions are best left out of consideration.

Since a convective layer is always some sort of boundary layer as well, the phenomena within it are subject to great modification by mechanical turbulence. While in special cases the mechanical source of turbulent energy is negligible, in most cases it must be taken into consideration along with the thermal source.

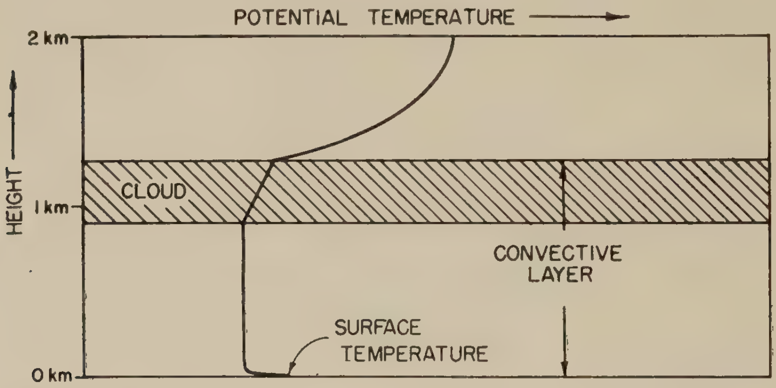

FIGURE 5. Schematic representation of convective air layer both warmed at surface and cooled at cloud top.

The information one could desire about convective layers falls into three rather distinct, but physically intimately related, categories: (a) The pattern of the convection. This may be either of an orderly nature, or of an irregular, turbulent nature. The pattern would be revealed, in part, by instantaneous sections, either horizontal or vertical, showing the distribution of velocity, temperature, or concentration. (b) The mean vertical distributions of temperature and concentration. (c) The mean vertical transfer of heat and of dissolved or suspended material.

Convective layers have received very little attention in spite of their widespread occurrence in regions of intense human activity. For the three categories mentioned above, which are pertinent to all five types of convective layers, only fragmentary bits of information exist. I am sure that the individual authors will agree with me that their papers do not offer general solutions, but, by describing isolated phenomena which call for explanation and generalization, mostly raise questions which remain unanswered. The purpose of this publication, then, is not so much to present results, as to focus attention on the almost untouched problems concerning convective layers. With this object, we have brought together a group of persons whose work has touched on various aspects of convective layers. If the results serve to stimulate a systematic attack on some of these problems, our work will have been well justified.

I should like to mention some phases of convective-layer problems which have received attention. Several investigators have carried out rigorous theoretical studies of convection patterns. Although these studies are confined to laminar flow, they appear to form a necessary background for work on the turbulent type of convection that occurs in the atmosphere and ocean. For this reason, the results of such studies are summarized in Mr. Stommel's paper, in a form that makes their basic features more accessible than do the original papers. A paper discussing theoretical aspects of the relation between convection patterns and wave patterns will be presented by Dr. Haurwitz.

The pattern of convection in the nocturnal type of convective layer in water has been studied by Langmuir (1938). The measurement of the vertical temperature distribution in this layer has become a routine operation, through the use of the bathythermograph, the first models of which were designed by Professor Spilhaus (1940). Papers on the mean vertical distribution of temperature in this layer, by Dr. Church and by Mr. Armstrong, are included, while Mr. Woodcock (1941) has studied the pattern of convection in the insolational type of convective layer in water.

The convection pattern of the convective air layer warmed at the surface is discussed by Messrs. Woodcock and Wyman, and by Mr. Raymond Wexler. For the lower part of this layer, observed vertical distributions of temperature have been previously recorded by Johnson and Heywood (1938) and Franssila (1945), and of water vapor, by Dr. Sverdrup (1946). For the upper part of the layer, a theory of the temperature distribution during cumulus convection was offered by Dr. Bjerknes (1938). New material on the distribution of temperature and water vapor in the layer warmed at the surface is here presented in a paper by Mr. Craig. The mean vertical transfer of heat in this layer has already been considered by Kampé de Feriet (1942), and by Burke (1945). Laboratory measurements of the mean vertical temperature distribution, both above and below an air-water surface, have also been made by Ramdas and Raman (1946).

With regard to future work on convective layers, guidance may be obtained from the methods used in the study of mechanical turbulence in boundary layers. By the clever choice of variables and parameters, widely varying problems have been brought under simple empirical laws. It appears probable that properly chosen measurements in convective layers in the ocean and atmosphere can be related to controlled laboratory experiments by means of quantities chosen in a similarly suitable manner, so that greater order will appear out of our scattered knowledge. A step in this direction was made years ago by Prandtl (1932), who suggested a law for the mean temperature distribution in a convective layer.

Finally, some mention may be made of important applications for which further knowledge of convective layers is needed. In the ocean, the vertical dispersion of heat, oxygen, and nutrient substances is accomplished in part by convection. There, too, convective layers play an important part in sound propagation. In the atmosphere, they have considerable influence on short-wave electromagnetic propagation.* Convection is a large factor in the dispersion of pollution (in water, as well as in air), and has a large influence on all other phases of the microclimatology of urban regions. Due to the daytime prevalence of a surface convective layer, the agricultural environment is intimately controlled by convection.

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Contribution No. 358

OBSERVATIONS OF VERTICAL TEMPERATURE AND HUMIDITY DISTRIBUTIONS IN THE CONVECTIVE LAYER ABOVE THE SEA SURFACE*

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During the summer and early fall of 1944, detailed soundings were made in the lowest 1000 feet of the atmosphere over Massachusetts Bay. This observational program was carried out, under the general direction of Mr. Donald E. Kerr, by members of Group 42, Radiation Laboratory, Massachusetts Institute of Technology. The measurements were primarily intended to be of assistance in studies concerning the effects of vertical gradients of temperature and humidity on the propagation of short radio waves in the atmosphere. The soundings and their interpretation were, however, essentially meteorological problems, despite their importance to propagation studies. Accordingly, several meteorologists, under the direction of Dr. R. B. Montgomery, participated in the project, helping to plan the measuring program and interpret the results.

The special nature of the propagation problem required very detailed measurements of temperature and humidity in that part of the atmosphere between the sea surface and about 1000 feet. Since meteorological upper-air instruments in common use are intended to sound in less detail a much larger layer of the atmosphere, new instruments were designed to meet the special requirements. The one developed at the Radiation Laboratory and used in making the observations to be presented here is called the *aeropsychrograph*, an electrical recording instrument which measures the dry-bulb and wet-bulb temperatures of the air. In some cases, it was carried aloft by an airplane, and about 500 soundings, most of them extending to 1000 feet, were obtained in this manner. At other times, the aeropsychrograph was carried aloft by a balloon to heights generally less than 500 feet, or run up the mast of a boat to about 50 feet. This instrument, as well as others developed for the same purpose, will be described in detail in a book to be published as part of a series describing wartime research at the Radiation Laboratory. The same book will include a discussion of the results of the measurements in Massachusetts Bay and of similar programs in other regions.[2]

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These soundings contain much that is of interest to meteorology itself, because they include measurements in the lower part of the atmosphere which are more detailed, in some respects, than any previously available. Some of the observations with a bearing on sea breezes have already been published.[1] Another meteorological problem on which they throw some light is that of the vertical distributions of temperature and humidity in air which is being heated from below by warmer water. It is the purpose of this paper to describe the distributions which were measured under such conditions, and to present and discuss specific examples of such soundings.

It was found that the convective layer above the sea surface contains three regions where the vertical distributions are essentially different. In a shallow layer near the surface, the temperature and humidity decrease rapidly with height. Above this, and extending throughout most of the layer, is a region where, within the accuracy of the observations, the air is mixed or homogeneous, that is, the lapse rate of temperature is adiabatic and the specific humidity is independent of height. At the top of the convective layer, the temperature distribution is hydrostatically stable, and the specific humidity generally decreases rapidly with height. When air passes over warmer water, the individual rates of change of the potential temperature and specific humidity of the air in the homogeneous layer are positive, as is that of the height of the convective layer.

A few selected soundings from among the many made are presented in FIGURES 1–5. Temperature and dew point are plotted against height above the surface, the broken lines representing the dry-adiabatic lapse rate of temperature and the vertical distribution of dew point which corresponds to constant specific humidity. Each airplane sounding consists of a series of measurements made between 20 feet and 1000 feet, and, in addition, a second series made between 20 feet and usually 500 feet, immediately afterward. The water temperature, indicated by an arrow in the figures, was generally determined, in the case of these selected soundings, by measurement from a boat at about the same time and place as the sounding. The wind force at the surface was estimated from the state of the sea by observers in the airplane.

FIGURES 1–3 all illustrate the degree of homogeneity found in the convectively stirred air. Between 20 feet and 1000 feet, the temperature deviates nowhere more than 0.5° F. from that corresponding to the adiabatic lapse rate. The deviations of dew point in FIGURES 1a and 2 appear to be larger, but it should be pointed out that, at the low dew points involved, these deviations correspond to very small changes in water-vapor content. To illustrate this, and to show an alternative method of presenting the observations, the sounding shown in FIGURE 1a is also presented in FIGURE 1b, where potential temperature (re-

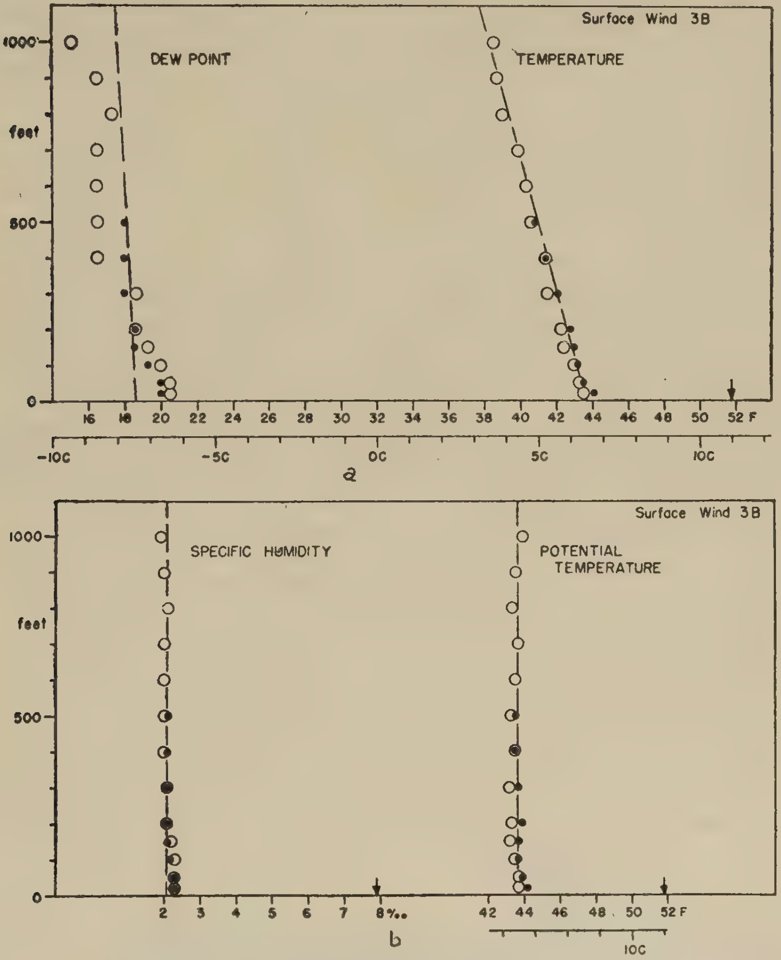

FIGURE 1. Airplane sounding showing homogeneity in the convective layer. 70° 36′ W, 42° 31′ N, 30 October 1944, ○ ascent 1410–1420 (time meridian 60° W), ● ascent 1423–1428, over-water trajectory (distance the air at 1000 ft. has travelled since leaving land), 8 miles.

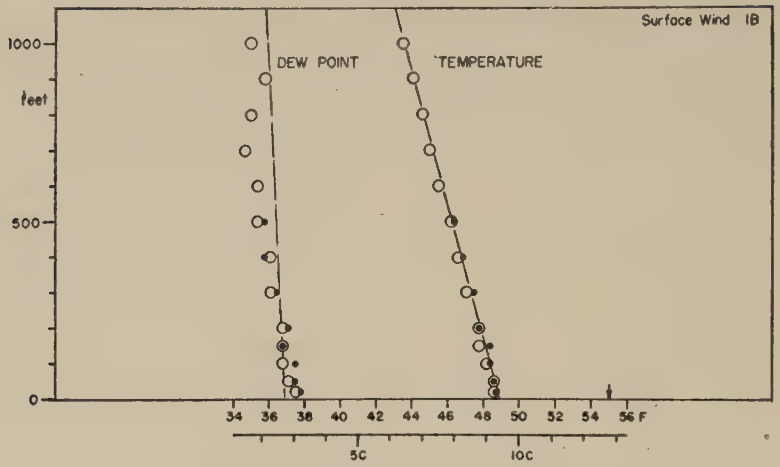

FIGURE 2. Airplane sounding showing homogeneity in the convective layer. 70° 27′ W, 42° 21′ N, 20 October 1944, ○ ascent 1528–1538, ● ascent 1541–1546, over-water trajectory more than 100 miles.

ferred to the surface, not 1000 mb) and specific humidity are plotted against height. Note that, in contrast to the homogeneity above 20 feet, very large vertical gradients must exist below 20 feet, as the temperature and dew point change in this layer from their values at the sea surface to those measured at 20 feet.

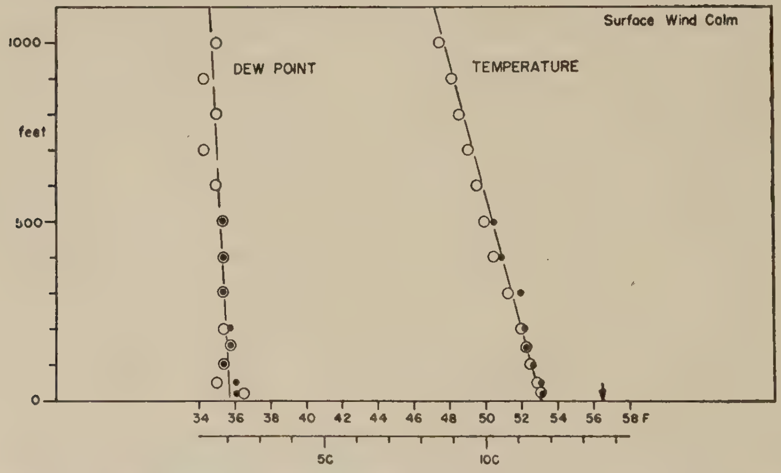

FIGURE 3. Airplane sounding showing homogeneity in the convective layer. 70° 20′ W, 42° 04′ N, 4 October 1944, ○ ascent 1200–1210, ● ascent 1220–1225, over-water trajectory 30 miles.

FIGURE 4 is a sounding in which the stable top of the convective layer appears. Again, a convectively mixed homogeneous layer is found, with large vertical gradients near the surface and above the convective

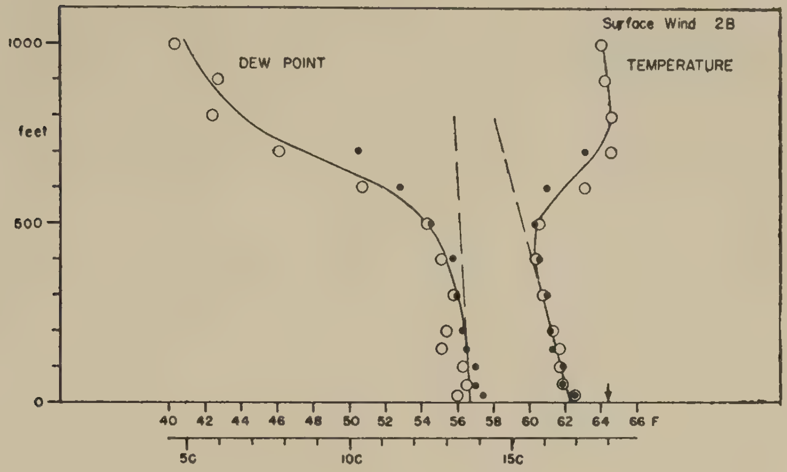

FIGURE 4. Airplane sounding showing stable top to the convective layer. 70° 16′ W, 42° 08′ N, 11 September 1944, ○ ascent 1113–1123, ● ascent 1132–1139, over-water trajectory 40 miles.

layer. The increase of temperature and decrease of humidity with height above the homogeneous layer are rapid, but show the effect of some mechanical mixing between the air above and the air below the top of the convective layer.

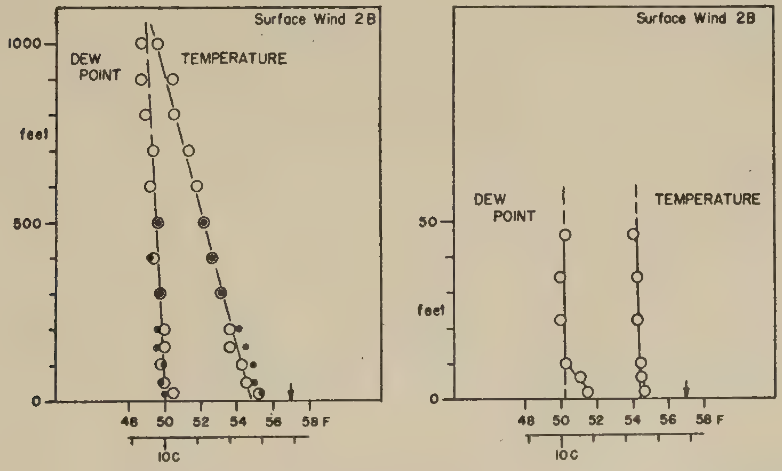

FIGURE 5. Airplane sounding showing homogeneity in the convective layer, and mast sounding showing large vertical gradients of temperature and humidity in lowest 10 feet. Airplane sounding: 70° 23′ W, 42° 17′ N, 10 October 1944, ○ descent 1202–1215, ● descent 1216–1223, over-water trajectory 25 miles. Mast sounding: 70° 23′ W, 42° 15′ N, 10 October 1944, ○ (average of two measurements) 1258–1310, over-water trajectory 25 miles.

In FIGURE 5a, another airplane sounding extending to 1000 feet shows homogeneous air in the convective layer. In this case, there is also shown (FIGURE 5b) a more detailed sounding of the lowest 50 feet, made from a boat at about the same time and place. The homogeneous distributions appear to extend down to about 10 feet, with a large part of the change taking place in the lowest 2 feet. It must be remembered, however, that the measured distributions in FIGURE 5b are not necessarily typical of those which might occur under different conditions of wind speed and temperature difference between air and water.

The height of the surface layer of large vertical gradients depends essentially on the temperature difference between the air and the water, and on the wind speed. It has proved impossible, for two reasons, statistically to determine the relationship from a study of the data. The water temperature often was not known within about 2° F., an appreciable percentage of the temperature difference between air and water for these observations. Moreover, the height of the surface layer could not usually be determined with much accuracy, since, in the airplane soundings, measurements were made at only two or three levels within the layer. However, the following statement can be made: In a series of 105 soundings in air heated over water, covering a range in wind force of 0 to 5 on the Beaufort scale and a range in temperature difference of 1° to 12° F., the superadiabatic lapse rate of temperature starting at the surface was observed to extend above 50 feet only four times and above 100 feet only twice.

The observations over Massachusetts Bay, and other similar observations made during the war, are of distinctive value. Detailed soundings of the layer between the surface and 1000 feet, or of a layer of comparable thickness at any height, have previously been neglected in favor of measurements nearer the surface of the earth or of observations of the gross vertical structure of the atmosphere to much greater heights. Moreover, the accuracy of these measurements, as indicated by their reproducibility and consistency, exceeds that of other upper-air soundings. Such detailed and accurate soundings should prove useful in many specialized research problems in meteorology.

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Contribution No. 359

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RADIATIVE COOLING IN THE LOWEST LAYERS OF AN ATMOSPHERE WARMER THAN THE GROUND

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(Manuscript received 30 September 1946)

ABSTRACT

Radiative cooling is computed for a warm, isothermal atmosphere streaming out over a cold surface. The study shows that the rate of cooling at heights from a few centimeters up to a few meters varies inversely as the square root of the distance from the ground, and that it varies somewhat more rapidly at larger distances.

The difference in radiative cooling at low levels between an isothermal and an adiabatic atmosphere is computed and found to be negligible in comparison with values derived from the isothermal atmosphere.

Comparison of radiative with observed cooling shows that radiative cooling is relatively small compared with cooling by turbulence in winds around 15 mph.

1. Introduction

When relatively warm air is brought into contact with a cool surface, it emits more radiation than it absorbs. Hence cooling is to be expected.

Cases of this type have been studied by Wexler [6] and Elsasser [3]. Wexler considered the formation of polar continental air over a snow surface, and Elsasser considered the cooling above a nocturnal inversion. Elsasser's results are equally applicable to ground inversions produced by advection of warm air over a cold ground. Both Elsasser and Wexler treated the mean cooling in layers having thicknesses of the order of 100 m.

In this paper, the rate of cooling is computed for specific levels from 100 m down to about 10 cm. The results are applied in a discussion of the conditions under which radiation can play an appreciable part in the cooling of warm air streaming out over cold water.

The general problem of cooling by infrared radiation has been treated by Elsasser [4]. He has constructed a chart from which mean cooling in atmospheric layers can be evaluated, provided that vertical distributions of the temperature and moisture are known.

The emission and absorption by water vapor and carbon dioxide are important for the radiative cooling in the lower layers of the atmosphere. In general, for polyatomic gases, emission and absorption are complicated functions of the thickness of substance traversed. For layers of air a few centimeters thick, emission and absorption vary linearly with the thickness [5]. For the layers of thickness between 10 cm (10^{-4} cm of precipitable water) and about 3 m (3×10^{-3} cm of precipitable water), both theory [4, 5] and observation [1, 2, 4] indicate that absorption and emission vary as the square root of the thickness. For still thicker layers, the relation becomes more complicated [4].

When the radiative properties of the atmosphere are horizontally homogeneous, the temperature variation is given by

$$\frac{dT}{dt} = -\frac{1}{c_p\rho}\frac{\partial F_N}{\partial z} \tag{1}$$

where T is temperature, t is time, c_p is specific heat at constant pressure, ρ is air density, F_N is net flux of energy, and z is the vertical coordinate.

If F_u and F_d are defined as the upward and downward flux, respectively, then $F_N = F_u - F_d$. Thus

$$\frac{dT}{dt} = -\frac{1}{c_p\rho}\left(\frac{\partial F_u}{\partial z} - \frac{\partial F_d}{\partial z}\right). \tag{2}$$

First, an isothermal atmosphere of temperature T_1 and constant specific humidity q superimposed upon a cooler ground of temperature T_0 will be considered. Under these conditions $\partial F_d/\partial z = 0$, since each layer absorbs as much downward radiation as it emits. Thus, equation (2) reduces to

$$\frac{dT}{dt} = -\frac{1}{c_p\rho}\frac{\partial F_u}{\partial z}. \tag{3}$$

2. Effect of water vapor

If the term du denotes the mass of water vapor contained in a vertical column of height dz and of unit area in horizontal cross section, $du = \rho q\, dz$. Thus, for water vapor, equation (3) may be written

$$\frac{dT}{dt} = -\frac{q}{c_p}\frac{\partial F_u}{\partial u}. \tag{4}$$

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[1] Contribution No. 359, Woods Hole Oceanographic Institution.

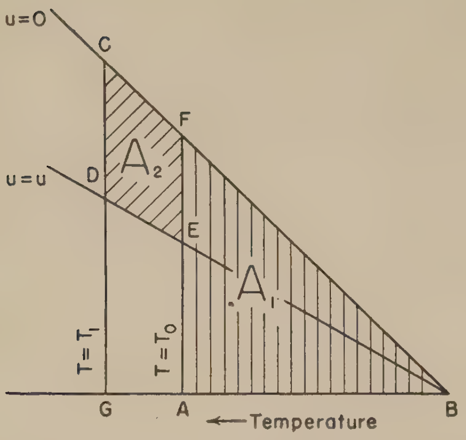

FIG. 1. Sketch based on the Elsasser radiation chart. The sum of the two hatched areas represents the upward flux.

At a level below which the mass of water vapor is u, the upward flux of radiation depends on the black-body flux at temperature T_0 and on the modification of this flux by the warmer intervening layer. On an Elsasser radiation chart, the upward flux is represented by the area ABCDEA (fig. 1). This area consists of two parts, A_1 and A_2. The symbols A_1 and A_2 will be used for the energies represented by the respective areas. Now A_1 is the black-body radiation of the ground and is not a function of u. Hence, from (4),

$$\frac{dT}{dt} = -\frac{q}{c_p}\frac{\partial A_2}{\partial u}. \tag{5}$$

From tables printed on the radiation chart, A_2 was plotted against $\sqrt{u}$ for $T_1 = 293\text{K}$ and $T_0 = 283\text{K}$. The result is a straight line for small values of u. The equation of this line is

$$A_2 = 3.2\sqrt{u}(T_1 - T_0) \tag{6}$$

where A_2 is in cal(3 hr)$^{-1}$cm^{-2}, and u is in g cm^{-2}. The equation is applicable at elevations from about 10 cm up to about 2.5 m (with specific humidity of 10 per mille).

For the range of u within which (6) holds, (5) may be written

$$dT/dt = -6.7\sqrt{q/\rho z}\,(T_1 - T_0) \tag{7}$$

where the unit of t is 3 hours, z is in cm, and ρ is in g cm^{-3}.

For elevations between 2.5 m and 70 m, the variation of A_2 with u is not given by a simple function; hence dT/dt was computed directly from equation (5) written in the form

$$\frac{dT}{dt} = -\frac{q}{2c_p\sqrt{u}}\frac{\partial A_2}{\partial\sqrt{u}}. \tag{8}$$

The quantity $\partial A_2/\partial\sqrt{u}$ was measured from a graph of A_2 against $\sqrt{u}$.

For elevations greater than 70 m there is again a simple relationship between A_2 and u, namely,

$$A_2 = (0.12 \ln u + 0.80)(T_1 - T_0) \tag{9}$$

where A_2 is in cal cm^{-2}(3 hr)$^{-1}$, u is in g cm^{-2}, and T is in centigrade. On substitution of equation (9) into equation (5), and application of $u = q\rho z$,

$$\frac{dT}{dt} = -\frac{4.0}{z}(T_1 - T_0) \tag{10}$$

where z is in meters and the unit of t is 3 hours. It is to be noted that this relation is independent of the value assumed for specific humidity.

The values of dT/dt were computed from equations (7), (8), and (10) with $T_1 = 293\text{K}$, $T_0 = 283\text{K}$, $q = 10$ per mille and 5 per mille, and $\rho = 1.25 \times 10^{-3}$ g cm^{-3}. The cooling due to water vapor is shown as a function of height by the solid lines in fig. 2.

3. Effect of carbon dioxide

The radiation chart cannot be used directly to compute the effect of carbon dioxide, because its construction is based on the assumption that the carbon dioxide in any layer absorbs and emits the same amount of radiation. When a temperature discontinuity exists, this assumption does not hold, and a procedure similar to that used by Elsasser [3] has to be employed. Again, equation (3) is applicable. Let $a(z)$ be the fraction of radiation absorbed in a layer of thickness z. Then the upward flux at an elevation z is given by the black-body radiation from the ground, σT_0^4, plus the energy emitted by the intervening layer, minus the energy absorbed by the intervening layer:

$$F_u = \sigma T_0^4 + a(z)\sigma(T_1^4 - T_0^4).$$

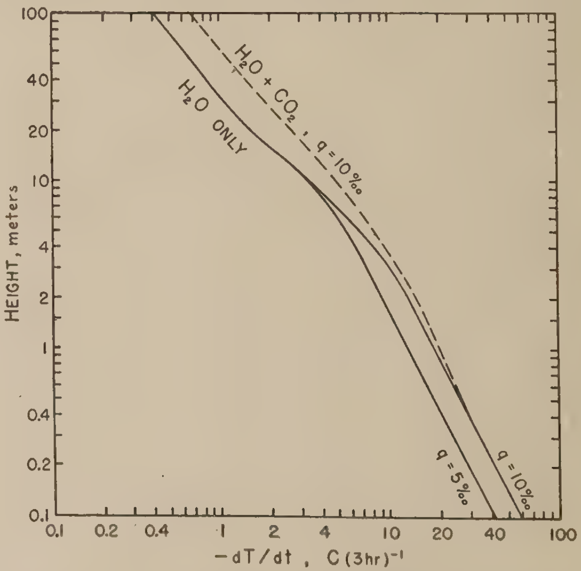

FIG. 2. Rate of radiative temperature change as a function of elevation for a temperature discontinuity of 10C at the ground.

Hence,

$$\frac{dT}{dt} = -\frac{1}{c_p\rho}\frac{\partial a}{\partial z}\sigma(T_1^4 - T_0^4). \qquad (11)$$

The absorption coefficient, a, has been measured by several investigators for unidirectional radiation. Since the radiation in the atmosphere is diffuse, these values cannot be used directly in equation (11). Elsasser [4] found that an absorption tube of length z absorbs the same fraction of unidirectional radiation as a layer of thickness 1.78 z absorbs of diffuse radiation, provided that a varies linearly with $\sqrt{z}$. This condition is satisfied for layers of air with normal carbon dioxide content for values of z between 4 m and 100 m. For thinner layers, the factor 1.78 has to be increased slightly, but for such layers the contribution of carbon dioxide to the total cooling is relatively unimportant. Hence, the factor 1.78 will be assumed to be valid for the whole range of thicknesses under consideration.

Let z' denote the length of an absorption tube having the same absorption coefficient as a layer of thickness z. Then $z' = 1.78\ z$. On substitution into (11),

$$\frac{dT}{dt} = -\frac{1.78}{c_p\rho}\frac{\partial a}{\partial z'}\sigma(T_1^4 - T_0^4).$$

The quantity $\partial a/\partial z'$ was determined from Elsasser's figure [4, fig. 26]. Since this figure is a graph of a against $\sqrt{z'}$, the slope on this graph divided by $2\sqrt{z'}$ yields the required value of $\partial a/\partial z'$.

The total cooling due to water vapor and carbon dioxide, for $T_1 = 293$K, $T_0 = 283$K, and $q = 10$ per mille, is given by a dashed line in fig. 2. It is nearly proportional to $\Delta T = T_1 - T_0$ and increases slowly with increasing mean temperature.

The cooling due to water vapor and, therefore, the total cooling vary only slowly with the specific humidity, as seen from fig. 2.

4. Comparison between an isothermal and a nearly adiabatic atmosphere

For comparison with observations, an atmosphere having a dry-adiabatic lapse rate is more suitable than an isothermal atmosphere. A nearly adiabatic atmosphere of the following specifications is assumed: ground temperature 10C, air temperature 20C, lapse rate dry-adiabatic from 1000 mb (ground) to 910 mb and halfway between dry-adiabatic and saturation-adiabatic from 910 mb up, specific humidity 10 per mille up to 930 mb and one per mille less than the saturation specific humidity at lower pressures.

This atmosphere was analyzed with the aid of Elsasser's radiation chart and compared with the isothermal atmosphere. In all layers analyzed (0–50 m, 0–100 m, 0–300 m), the mean rate of cooling due to water vapor in the adiabatic atmosphere exceeded that in the isothermal atmosphere by 0.2 C(3 hr)$^{-1}$. Since the value is the same for layers of widely varying thickness, it expresses the difference between the cooling in the two atmospheres not only in the mean of these relatively thick layers, but at specific elevations as well.

It is seen from fig. 2 that below about 40 m this difference in cooling between an isothermal and an adiabatic atmosphere of the same surface temperature and specific humidity may be neglected.

5. Comparison with observation

Fig. 2 shows that the total *radiative* cooling at 6 m is 7.2 C(3 hr)$^{-1}$ or 0.4C in 10 min. Since the assumed initial discontinuity is 10C, this amounts to a modification of 4 per cent in 10 min. The computation was made under the assumption that during the 10 min the radiative cooling is constant and equal to its initial value. Actually, the cooling decreases rapidly for two reasons: the temperature of the air at 6 m approaches the ocean temperature, thus decreasing ΔT; and the air above 6 m becomes warm relative to the air at 6 m. Thus the cooling of 4 per cent given above is an upper limit.

Three soundings[2] taken 2–3 miles from shore, in offshore winds with speeds near 15 mph, show that the initial temperature discontinuity between the ground and the air at an elevation of 6 m had been decreased, on the average, by 20 per cent in the first 10 min over the sea. This value is much larger than that to be expected from cooling due to radiation alone. It is probable that most of the cooling was caused by eddy conduction and that radiation played only a minor role. This conclusion is strengthened by the fact that the specific humidity is modified to about the same extent as the temperature.

At lower wind speeds, turbulence is less important. However, no observations are available for a determination of the critical wind speed below which the effect of radiation exceeds that of turbulence.

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[2] These soundings were obtained by the Radiation Laboratory of the Massachusetts Institute of Technology and analyzed by Richard A. Craig at the Woods Hole Oceanographic Institution.

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POISONING AND RECOVERY IN BARNACLES AND MUSSELS[1]

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Introduction

Previous investigations have shown that the prevention of the attachment of organisms to ships' hulls by antifouling paint is related to the rate of solution of the toxic material, and hence, to its concentration in the sea water at the paint's surface (Ketchum, Ferry, Redfield, Burns, 1945). The present investigation was undertaken to test the effectiveness of different metallic salts as poisons for two important types of fouling organisms and to evaluate them under conditions in which the concentration and ionic form of the toxic materials were accurately known. In earlier attempts to test lethal action, supposedly toxic materials have been incorporated in paints applied to test-panels or to the inside surfaces of containers and the degree of fouling resistance noted, but in most cases no adequate measure was made of the concentrations of the toxics which were actually emitted by the paint. In other tests, fouling organisms were placed in containers of sea water to which known amounts of toxics had been added but without adequate knowledge of the ionic transformation of the toxics which ensue in the presence of sea water (Bray, 1919; Edmondson and Ingram, 1939; Orton, 1929–30; and Parker, 1924).

We proposed, therefore, to conduct direct tests of the action of various individual metals in graded concentrations and in different chemical forms, on two important types of fouling organisms; namely, barnacles and mussels. We desired also to investigate the relationship between the concentration of various toxics and the exposure time necessary to kill, in order to ascertain the most efficient concentration of the poison for the destruction of fouling organisms.

A second purpose was to follow the course of poisoning and recovery in barnacles and mussels when copper was used as the poison. It was desired to measure the amount of copper in the tissues and to discover whether death from copper poisoning was brought about specifically by the accumulation of a certain amount of the poison in the tissues or by the entrance of the copper into the body at a certain rate or for a critical period of time. Finally, it was desired to ascertain from how great a dose of copper an animal could recover, and to learn whether, after recovery, the animal was more or less susceptible to subsequent exposures of the toxic.

I am indebted to Mrs. Dayton Carritt for assistance in carrying out the experiments, to Mrs. Barbara Mott Ferry for chemical analyses, to Dr. John Ferry and Dr. Gordon Riley for furnishing toxics, and to Mr. Porter Smith for technical assistance. I am indebted to the University of Miami for the use of facilities at the

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[2] Contribution Number 360.

Marine Laboratory. I also wish to thank Dr. Walton Smith and Dr. Charles Pomerat for valuable cooperation.

OBSERVATIONS ON ADULT BARNACLES AND MUSSELS

The effectiveness of various poisons was investigated first using the barnacle as a test animal, since the barnacle is generally the most serious offender as a fouling organism. Adult barnacles were employed for the majority of the experiments at Woods Hole, but one set of tests was conducted on nauplii which had been discharged in a laboratory tank. Although attachment of the barnacle takes place previous to the adult stage, there is evidence that a poisoned barnacle is less securely attached than a normal animal and may be more easily dislodged. Special interest centers about the poisoning of the cyprid, since this is the attaching stage. In view of the fact that cyprids could not be obtained in sufficient numbers at Woods Hole, experiments on this stage were conducted at Miami Beach, Florida. Mussels, which are of relatively large size, were found advantageous for other tests, especially those involving the copper assay of living tissue.

Source and preparation of material

Certain of the present tests were carried out with *Balanus balanoides* growing on stones obtained near low tide mark at Woods Hole. In later tests *Balanus eburneus* was employed, obtained through the kindness of Dr. Stanley Cobb, from a wharf in Cotuit Harbor. Parts of the wharf were removed and transported to the laboratory tanks. The barnacles were kindly identified by Dr. Richard McLean.

For the experiments with *B. balanoides* the material was collected on the same day that the tests were begun. Single stones bearing 10 to 30 barnacles (ranging from 3 mm. to 10 mm. in diameter) were placed in individual beakers or culture dishes containing from 250 cc. to 500 cc. of sea water with or without toxic. For the work using *B. eburneus,* a stock of animals attached to fragments of wood was maintained in large battery jars provided with running sea water. In preparation for the tests it was necessary to split and saw the pieces of wood into blocks of convenient dimensions. Blocks about 4 cm. to 6 cm. square, each bearing 10 to 20 barnacles ranging from 4 mm. to 20 mm. in diameter, were similarly placed in individual containers. In other experiments larger blocks bearing several hundred barnacles were placed in battery jars of 8 liters capacity or more.

With both species of barnacles it was found that when the sea water was renewed daily, the animals in the individual containers remained in a healthy condition for several weeks. There were evidently enough food particles in the sea water supplied to provide a maintenance diet. Faecal material was produced in abundance but the barnacles grew little, if at all.

The mussels employed were the common species in the Woods Hole region, *Mytilus edulis,* obtained from the dock and float of the Oceanographic Institution. The mussels were placed individually or in batches in culture dishes or large battery jars. The animals began attaching their byssus threads to the bottoms or sides of the containers almost immediately. If the sea water was renewed each day, the mussels continued in healthy condition indefinitely, apparently obtaining sufficient nutriment from the food particles present in the sea water.

Behavior during poisoning

When barnacles were placed in the toxic media, they opened their shells and began raking or filtering the water with their cirri as soon as did the controls in fresh sea water. Ordinarily this took place within a few minutes. If the concentration of the poison was such as to kill the barnacle within two or three days, the animals would begin to show signs of bad condition after about 12 hours. The first symptom was the slowing down of the beat of the cirri and soon thereafter their sweep became reduced in extent. As poisoning progressed, the movement of the cirri became still slower and more curtailed until they opened to only one-half or one-quarter of their usual scope. When the poisoned barnacle stopped filtering, it tended to come to rest with the cirri half extended, in contrast to the healthy animal in which the cirri are drawn completely in and the shell tightly closed during rest. In the poisoned animal, the shell could at first be caused to close by prodding it with a needle. After further poisoning, when no response could be elicited by stimulation with the needle, the barnacle was considered dead. The following symbols are used in the tables to designate these conditions:

++++	normal rapid sweep of cirri
+++	full sweep but slow
++	incomplete sweep
+	open, inactive, but reacts to touch
0	dead

If the barnacle was replaced in fresh sea water (preferably running sea water) within a day of the time it reached the next to last condition (+), it would usually recover completely its full activity after a few days.

In the case of the mussel, the change in condition as poisoning progressed was less easily observed. In the higher concentrations of the toxics, the animals failed to attach themselves to the walls of the containers and tended to remain closed for long periods. When placed in weaker solutions, however, many of the mussels became strongly attached and remained with their shells open to the normal extent to allow the inflow and outflow of water. In either case, after poisoning had progressed to a certain point, the valves were found gaping wide open. When this condition was first reached, the animal responded to prodding by closing slowly. A day later, or less, no response would follow such stimulation and the animal was considered dead. Once the mussel reached the stage in which it gaped open more than normal, though it might still react, it would not recover when placed in fresh sea water. In fact, mussels were frequently observed to die many days after having been transferred from the toxic solution into fresh sea water although outwardly they appeared to be in normal condition in the interim.

Toxicity of various metallic salts to barnacles

The toxicity of the following metals was investigated: copper, mercury, silver, and zinc. The last three of these was tested as the ions which resulted from the introduction into the sea water of $HgCl_2$, $AgSO_4$, and Zn $(NO_3)_2$ respectively. The copper, on the other hand, was tested not only in the form of basic cupric carbonate, but also as cupric citrate, cupric tartrate, cupric salicylate, and cupric para aminobenzoate. The interest in these other compounds of copper lies partly in the possibility of revealing important differences in toxicity. Of further significance is the fact that these substances are much more soluble in sea water than is basic cupric carbonate. Therefore, when copper is supplied in the form of these more soluble ions, it is possible to establish a high concentration of the toxic in the water adjacent to the surface from which the material is free to dissolve.

Individuals of *Balanus balanoides* were placed in beakers or jars containing graded concentrations of toxics in sea water with a control for each series. Since the media were renewed each day, the danger of significant changes in concentration due to such causes as adsorption was minimized. The minimum concentrations necessary to kill 90 per cent of the barnacles after continuous exposures of two days and five days are indicated in Table I. Among the various forms of copper, the basic cupric carbonate was the most effective but the concentrations of the citrate and tartrate necessary to kill were only slightly greater. The toxicity of silver as silver sulphate was of the same order of magnitude but somewhat greater concentrations of mercury as mercuric chloride were required. The effectiveness of zinc, on the other hand, was very much less than any of the other substances tested (*cf.*, Riley, 1943).

TABLE I

The concentrations of various metallic salts necessary to kill 90 per cent of adult barnacles after continuous exposures for the indicated periods. Concentrations are expressed as milligrams of metal per liter of sea water

	Toxic	Concentration lethal in 2 days	Concentration lethal in 5 days
		mg./liter	mg./liter
Series I			
	Basic Cu Carbonate	0.35	—
	Basic Cu Carbonate	0.48	—
Balanus balanoides	Cu Citrate	0.60	0.18
from	Cu Citrate	0.60	0.30
Woods Hole harbor	Cu Tartrate	0.58	0.17
	$HgCl_2$	1.0	0.5
	Ag_2SO_4	0.4	0.2
	$Zn(NO_3)_2$	32.	8.0
Series II			
	Basic Cu Carbonate	0.28	0.14
Balanus eburneus	Cu citrate	0.55	0.14
from	Cu salicylate	0.90	0.45
Cotuit harbor	Cu para aminobenzoate	—	0.50

Experiments with *Balanus eburneus* indicated similarly that the lethal action of cupric citrate is somewhat less than that of basic cupric carbonate although the magnitude of the difference is not great. The toxicity of cupric salicylate and cupric aminobenzoate were somewhat less than the citrate.

In view of the fact that the toxicity of cupric citrate was found to be almost as great as that of basic cupric carbonate, and since stock solutions of higher and less variable concentrations could be maintained, the tests which follow were conducted with the citrate.

Relation between concentration of cupric citrate and killing time

Barnacles

With the higher concentrations of cupric citrate in which killing occurred within a few days, adult barnacles all succumbed at about the same time, but at the lower concentration it was difficult to determine accurately when the barnacles should be considered dead. At still greater dilutions of the toxic, it was found that most of the animals lived on in a feeble condition for two or three weeks or more. Furthermore, there was considerable variation from experiment to experiment, which was no doubt due not only to individual differences in the batches of barnacles, but also to unavoidable changes in the seasonal condition and in the age of the animals. No consistent trend appeared in relation to the latter conditions except that barnacles in the nauplius stage were killed much more quickly than the adults, as noted below.

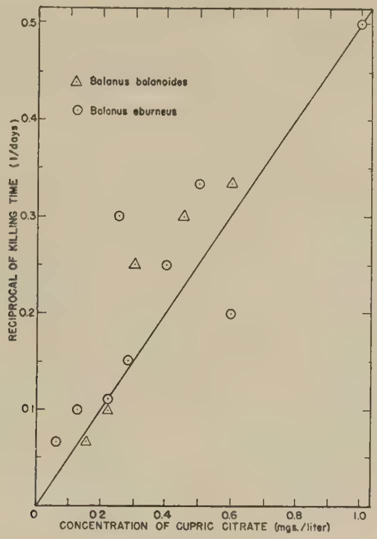

FIGURE 1. The relation between killing time and concentration of toxic for two species of barnacles.

For both *B. balanoides* and *B. eburneus,* the killing time ranged between two and five days for concentrations of 0.60 to 1.00 mg. Cu/liter. At 0.22 mg./liter the animals succumbed after ten days. At concentrations of 0.06 mg./liter and less, the animals remained alive for two weeks or more. When the reciprocal of the killing time was plotted against the concentration, as in Figure 1, a roughly linear relation was found. The approximate linearity of this relation indicates that the rate of action of the poison is directly proportional to its concentration.

The results of a series of tests on the poisoning of nauplii, made on the day of their release from the brood pouch, are shown in Table II. They indicate that the

TABLE II

Effect of concentration of cupric citrate on the survival of nauplii of Balanus eburneus. August 25–27, 1942

Concentration mg. Cu/liter	After 22 hrs.	After 29 hrs.	After 48 hrs.
1.00	all dead	—	—
0.50	all dead	—	—
0.25	all dead	—	—
0.13	75% alive	all dead	—
0.06	75% alive	50% alive	1% alive
0.03	100% alive	95% alive	5% alive
Control	100% alive	95% alive	5% alive
Control	100% alive	95% alive	10% alive

nauplii are killed after much shorter exposure than is the case with the adults. The test was not very satisfactory because the controls lived for only about two days.

Mussels

The experiments on the mussel, *Mytilus edulis,* indicate that it is much more sensitive to cupric citrate than the barnacle (Tables III and IV). A half-day exposure to 0.55 mg. Cu/liter was sufficient to kill the three mussels in this concentration. One animal in each of the experiments succumbed following a half-day exposure to a concentration of only 0.14 mg. Cu/liter. With adult barnacles, exposures of two days and five days are required for killing at these concentrations. In these tests, and in many others with mussels, death did not ensue until several days after the animals had been transferred to fresh sea water. In one case the mussel did not die until the tenth day following a half-day exposure to the poison. In most cases the animals showed no outward sign of unhealthy condition in the interim.

TABLE III

Relation of killing time to concentration of cupric citrate in the mussel, Mytilus edulis. In each test three animals (about 3 cm. long) were placed in each toxic solution for the periods indicated and then transferred to fresh sea water. Started August 6, 1942

Concentration mg. Cu/liter	Time in toxic days	Killing time days
0.55	½	4, 8, 10
	1	2, 3, 4
	2	2, 3, 3
	3	2, 3, 3
0.14	½	4, *, *
	1	3, 3, 4
	2	3, 4, 4
	3	3, 4, 4

* Still alive when experiment terminated on August 18.

TABLE IV

Relation of killing time to concentration of cupric citrate in the mussel, Mytilus edulis. In each test two animals (about 3 cm. long) were placed in each toxic solution for the periods indicated and then transferred to fresh sea water. Started August 10, 1942

Concentration mg. Cu/liter	Time in toxic days	Killing time days
0.14	½	5, *
	1	3, 4
0.08	½	*, *
	1	*, *
	2	6, 8
0.04	½	*, *
	1	*, *
	2	*, *
	3	8, *
0.02	1	*, *
	2	*, *
	4	*, *

* Still alive when experiment terminated on August 20.

Accumulation of copper in barnacle tissues during poisoning and recovery

Several series of experiments were undertaken to determine the extent to which copper accumulated in the tissues of the barnacles subjected to solutions of cupric citrate. Since the shell material of the barnacle is several times greater in volume and many times greater in dry weight than the soft tissues, a technique was developed for the copper assay of both constituent parts of the animal separately. The number of barnacles used for a single analysis varied from 15 to 40 with the size and expected copper content. In the earlier experiments, the animals were chiseled free from the substratum, but in so doing all the fluid material was lost, and bits of broken shell were sometimes included with the soft parts. In the later experiments the soft tissues were taken from the shell without disengaging the animals from the substratum by removing the operculum and picking out the soft parts with forceps. The fluid material, which was removed with a pipette, and the tissues were then placed in a weighed Erlenmeyer flask. In the case of mussels, a much smaller number of animals was used. The relatively large amount of sea water within the mantle cavity of the mussel was drained off and discarded before removing the soft parts.

The wet weight of the soft tissues of barnacles and mussels was obtained and the approximate volume of the wet tissue was determined by forcing it into a graduated cylinder.[3] The material was transferred quantitatively to a flask, dried in an oven at 100° C., and the dry weight determined. Enough H_2SO_4 was added to char the material. It was heated to fumes on a hot plate, and concentrated HNO_3 was added dropwise until a colorless solution was obtained. The solution in the flask was transferred quantitatively to a 100 cc. volumetric flask and diluted to the mark. Test for copper was made by the carbamate method (Coulson, 1937). A blank to which the same amount of reagent was added was also carried through the above procedures. In the analysis of barnacle shells, the wet weight of the shells was first determined. The shells were then dried in the oven at 100° C. overnight and the dry weight determined. The material was ignited in the muffle furnace at 800°–900° C. for three hours, removed and cooled. Two cubic centimeters of concentrated HCl were added, warming if necessary to dissolve.[4] The remainder of the analysis followed the same procedure as with the soft tissues.

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[3] In the early experiments, volume in cubic centimeters alone was determined, but was subsequently found to be very nearly equal to the wet weight in grams.

Determinations revealed that the amount of copper in the shell tissue of both normal and poisoned barnacles was quite variable. There was also no consistent change in the copper content of the shells in the case of batches of poisoned barnacles with increasing amounts of copper in the soft tissues. Accordingly, in the later experiments the laborious and rather unsatisfactory copper assay of the shells was omitted.

The copper content of barnacles freshly brought into the laboratory is many times greater than an equal volume or an equal weight of sea water (Table V). Evidently under natural conditions, the barnacle tends to accumulate copper in its tissues to a considerable extent.

TABLE V

Copper content of freshly collected barnacles
Woods Hole sea water contains 0.00001 to 0.00003 mg./cc.

Species	Source	Number	Copper in soft parts			Copper in shells		
			mg.	mg./cc.*		mg.	mg./cc.	
Balanus eburneus	Cotuit, July 28	50	0.0017	0.0014		0.141	0.027	
	Cotuit, July 28	50	0.0027	0.0024		0.097	0.014	
			mg.	mg./g. Wet wt.	mg./g. Dry wt.	mg.	mg./g. Wet wt.	mg./g. Dry wt.
Balanus eburneus	Cotuit, Aug. 20	50	0.015	0.0038	0.008	0.007	0.0003	0.0004
	Cotuit, Aug. 20	40	0.010	0.0019	0.014	—	—	—
	Cotuit, Sept. 12	30	0.016	0.0011	0.016	—	—	—
Balanus balanoides	Woods Hole, July	100	0.029	0.029	0.104	0.069	0.0070	0.0075
	Buzzards Bay	50	0.023	0.027	0.068	0.063	0.0065	0.0067

* May be assumed equivalent to mg./g. wet weight.

In experiments designed to test whether barnacles could accumulate copper in their tissues, it was found that the amount of copper present increased rapidly for each day that the animals remained in the toxic solution. At the end of four days of continuous poisoning in the two concentrations used, all the animals were dead (Blocks A and C, Tables VI and VII). However, in those cases in which the barnacles were transferred to fresh sea water after one or two days, the animals were restored to what appeared to be a healthy condition.[5] Analysis of the tissues of the barnacles which had been replaced in fresh sea water showed that the animals had not only recovered their activity but also had eliminated a certain amount of copper. These barnacles still contained, however, as much as twenty-five times the amount of copper found in their tissues before poisoning began.

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[4] If an excess of $CaCO_3$ remained, more acid was added until evolution of CO_2 ceased.

[5] The recovery of Bugula larvae from copper poisoning was reported by Miller and Cupp (1942) and Miller (1946).

TABLE VI

Changes in copper content of soft tissues during poisoning and recovery

Toxic: Cupric citrate, conc. 0.20 mg. Cu/liter
Test Animal: Balanus eburneus
Date: August 3–8, 1942
*Basis: Copper content per cubic centimeter of soft tissue **

Block A		Block B	
Initial copper content	0.010 mg.	Initial copper content	0.010 mg.
After 1 day in toxic	0.034 mg.	After 1 day in toxic	0.034 mg.
After 2 days in toxic	0.070 mg.	After 1 day in sea water	0.033 mg.
After 3 days in toxic	0.093 mg.	After 2 days in sea water	0.030 mg.
After 4 days in toxic	0.112 mg.	After 3 days in sea water	0.035 mg.
		After 4 days in sea water	0.026 mg.
Condition at end—dead		Condition at end—open, inactive but reacts to touch	

* May be assumed equivalent to wet weight.

TABLE VII

Changes in copper content of soft tissues after varying exposures to toxic and after recovery

Toxic: Cupric citrate, conc. 0.35 mg. Cu/liter
Test Animal: Balanus eburneus
Date: August 10–17, 1942
*Basis: Copper content per cubic centimeter of soft tissue **

Block C		Block D		Block E	
Initial Cu content	0.002 mg.	Initial Cu content	0.002 mg.	Initial Cu content	0.002 mg.
After 1 day in toxic	0.024 mg.	After 1 day in toxic	0.024 mg.	After 1 day in toxic	0.024 mg.
After 2 days in toxic	0.073 mg.	After 2 days in toxic	0.073 mg.	After 1 day in sea water	0.029 mg.
After 3 days in toxic	0.089 mg.	After 1 day in sea water	0.056 mg.		
After 4 days in toxic	0.075 mg.				
		After 9 days in sea water	0.054 mg.	After 6 days in sea water	0.022 mg.
Condition at end—dead.		Condition at end—cirri give incomplete sweep or full sweep but slow.		Condition at end—normal rapid sweep of cirri.	

* May be assumed equivalent to wet weight.

These indications that barnacles can take up relatively large quantities of copper without being killed and can eliminate the poison to a certain extent were confirmed by more elaborate experiments which were designed primarily to test the effects of the toxic and of different periods of exposure and of recovery (Tables VIII to XI).[6] These experiments demonstrated that barnacles took up copper

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[6] In these experiments the dry weight of the soft tissues to be analyzed was determined and the copper content stated on the more accurate basis of milligrams of copper per gram of dry weight. The dry weight for the soft parts of the barnacle was found to be about 5 per cent to 20 per cent of the wet weight. Since this group of experiments was conducted during late summer and autumn, there exists the possibility that the results may not be strictly comparable with the earlier work. The barnacles tested were necessarily older and larger, and were no doubt in a different physiological condition. It was noted that the animals became less active as the season progressed, and by late autumn they tended to remain closed for long periods. This last fact alone would be expected to cause an important difference in the rate at which toxic was absorbed. In general, the animals tended to survive longer in high concentrations of toxic in the autumn than they had in the summer.

TABLE VIII

Comparison of changes in copper content of soft tissues during continuous exposure to low concentration of toxic and intermittent exposure to higher concentration

Toxic: Cupric citrate, Block F: 0.14 mg. Cu/l.; Block G: 0.22 mg. Cu/l.
Test Animal: Balanus eburneus
Date: August 24 to September 28, 1942
Basis: Copper content per gram of dry weight of soft tissue
Exposure times indicated for toxic are cumulative totals

Block F		Block G	
Initial copper content	0.014 mg.	Initial copper content	0.008 mg.
After 1 day in toxic	0.05 mg.	After 1 day in toxic	0.037 mg.
After 2 days in toxic	0.08 mg.	(Replaced in sea water for 1 day)	—
After 7 days in toxic	0.33 mg.	After 2 days in toxic	0.095 mg.
After 15 days in toxic	1.09 mg.	(Replaced in sea water for 1 day)	—
(Replaced in fresh sea water)		After 3 days in toxic	0.18 mg.
After 18 days in sea water	0.39 mg.	(Replaced in sea water for 6 days)	—
		After 4 days in toxic	0.23 mg.
			(0.19 mg.)*
		(Replaced in sea water for 7 days)	0.17 mg.
		After 7 days in toxic	0.48 mg.
		(Replaced in sea water for 16 days)	0.51 mg.
Condition at end—full but slow sweep of cirri		Condition at end—full but slow sweep of cirri	

* Batch of dead barnacles.

faster from the more concentrated toxic media. With the slower rate of absorption at the lower concentrations, the animals appeared to withstand higher amounts of copper in their tissues. Thus the highest copper content observed for living barnacles, namely, 1.09 mg. per g. dry weight, was found after fifteen days in 0.14 mg. Cu/liter cupric citrate (Table VIII, Block F). In cases in which large amounts of copper were absorbed the barnacles tended to live longer and to remain in better condition when periods in sea water were alternated with periods in the toxic medium.

In cases where the copper content was determined for the dead barnacles, which were found among the living individuals in increasing number as the experiment progressed, it was almost invariably true that the amount of copper present was less than that for the living specimens from the same block. This observation suggests that the entrance of copper and its fixation in the tissues of the barnacle is not simply a mechanical process of diffusion or adsorption but is a process which is influenced in some way by the metabolic reactions of the living organisms.

Due to the facts considered above, it is not possible to arrive at any definite value for an absolute amount of copper which must be absorbed by the barnacle to kill it, nor at any rate of absorption above which death will ensue. The results suggest that killing may not be due to the destruction of some vital substance or process by the direct action of the copper as much as to a general depressing action of the toxic on some function, such as the feeding reaction, to the extent that death eventually follows.

TABLE IX

Comparison of changes in copper content of soft tissues during continuous and intermittent exposures to high concentration of toxic and continuous exposure to lower concentration

Toxic: Block H—Cupric citrate 0.75 mg. Cu/l. Continuous
Block I—Cupric citrate 0.35 mg. Cu/l. Continuous
Block J—Cupric citrate 0.75 mg. Cu/l. Alternating daily with sea water
Test Animal: Balanus eburneus
Date: September 21 to October 14, 1942
Basis: Copper content per gram of dry weight of soft tissue

Block H		Block I	
Initial Cu content	0.016 mg.	Initial Cu content	0.016 mg.
After 2 days in toxic	0.17 mg.	After 3 days in toxic	0.13 mg.
After 4 days in toxic	0.30 mg.	After 6 days in toxic	0.25 mg.
After 6 days in toxic	0.38 mg.	After 9 days in toxic	0.32 mg.
After 7 days in toxic	(0.33 mg.)*	After 11 days in toxic	0.76 mg.
After 8 days in toxic	0.48 mg.	After 14 days in toxic	(0.39 mg.)*
After 11 days in toxic	(0.84 mg.)*	After 14 days in toxic	0.49 mg.
		After 18 days in toxic	(0.43 mg.)*
		After 18 days in toxic	0.60 mg.

Block J		
Initial Cu content		0.016 mg.
After 2 days in toxic,	1 day in sea water	0.16 mg.
After 4 days in toxic,	3 days in sea water	0.13 mg.
After 6 days in toxic,	6 days in sea water	0.31 mg.
After 8 days in toxic,	7 days in sea water	0.42 mg.
After 8 days in toxic,	8 days in sea water	0.25 mg.
After 10 days in toxic,	9 days in sea water	0.48 mg.
After 12 days in toxic,	11 days in sea water	0.50 mg.
After 12 days in toxic,	11 days in sea water	(0.48 mg.)*

* Batch of dead barnacles.

TABLE X

Changes in copper content of soft tissues during recovery from various exposures to toxic

Toxic: Cupric citrate 0.75 mg. Cu/l.
Test Animal: B. eburneus
Date: October 21–November 12, 1942
Basis: Copper content per gram of dry weight of soft tissue

	Treatment	Copper content	Condition
Block L	After 3 days in toxic	0.38 mg.	++
	After 10 days in sea water	0.31 mg.	+
	After 14 days in sea water	0.21 mg.	+
Block M	After 6 days in toxic	0.38 mg.	+
	After 7 days in sea water	0.36 mg.	+
	After 14 days in sea water	0.40 mg.	++
Block N	After 9 days in toxic	0.58 mg.	0+
	After 9 days in toxic	(0.39 mg.)	dead individuals
	After 7 days in sea water	0.43 mg.	+
	After 14 days in sea water	0.39 mg.	++

No barnacles were found to have been killed by the absorption of less than 0.19 mg. of copper per g. of dry weight—an amount which is ten or more times the normal content of the tissues. In many cases animals succumbed after about 0.4 mg. per gram of dry weight had been taken up by the tissues. In no case did the barnacles absorb more than 1.09 mg. of copper per gram of dry weight. Barnacles which had accumulated copper from toxic solutions to the extent of 0.5 mg. to 1.09 mg./g. dry weight, in some cases revived when replaced in fresh sea water and were still alive two or three weeks later. At the end of the period, when they had regained normal, or nearly normal, activity, they contained 0.3 to 0.5 mg. of copper per g. of dry weight. In most instances the barnacles eliminated copper from their tissues, especially in cases where a high concentration had been accumulated. Although the copper which had been absorbed was never entirely eliminated, and although the process was slower than for accumulation, the experiments show that barnacles have some ability to rid their tissues of copper.

TABLE XI

Changes in copper content of soft tissues during recovery from exposures at high concentrations of toxic

Toxic: Block O—Cupric citrate 0.90 mg. Cu/l.
Block Q—Cupric citrate 0.75 mg. Cu/l.
Test Animal: B. eburnesus
Date: October 21–November 21, 1942
Basis: Copper content per gram of dry weight of soft tissue

	Treatment	Copper content	Condition
Block O	After 8 days in toxic	0.52 mg.	0+
	After 8 days in toxic	(0.48 mg.)	dead individuals
	After 8 days in sea water	0.42 mg.	0+
Block Q	After 9 days in toxic	0.53 mg.	0+
	After 9 days in toxic	(0.35 mg.)	dead individuals
	After 8 days in sea water	0.40 mg.	+
	After 15 days in sea water	0.35 mg.	++

Accumulation of copper in mussel tissue during poisoning and recovery

To determine the amount of copper taken up by the tissues of the mussel when subjected to copper solutions, groups of 25 mussels were placed in various concentrations of cupric citrate and were later transferred to fresh sea water after increasing periods of time. The media were renewed every day. The copper content of 20 fresh animals from the same source was assayed at the beginning of the experiment and batches of three to five animals were withdrawn from the various groups for copper assay after the indicated number of days during poisoning and during recovery (Table XII).

The initial copper content of the mussel tissue was 0.0109 mg. per gram of dry weight, roughly the same as for the barnacle. Since the wet weight of the soft parts of the mussel was similarly found to be about ten times the dry weight, it is clear that the fresh mussel also contains many times the concentration of copper present in the sea water.

After the first day in the toxic media, the mussels in the more concentrated solutions had taken up six to eight times their original amount of copper, but in the weaker solutions, there was no consistent increase in copper content until after an exposure of three days. The group of mussels (Group 4) in the weakest solution had absorbed only about two and one-half times their initial copper content after five days—or less than half the amount the Group 1 mussels had absorbed in one day in a solution five times as strong. In addition, the mussels were found to be able to rid their tissues of copper effectively. One day's sojourn in fresh sea water was sufficient to reduce the amount of copper in the mussels from the strongest solutions by more than 70 per cent. In cases where longer exposures were employed (although in lower concentrations) more time seemed to be required for the elimination of the copper—perhaps because it had penetrated to deeper tissues. At the end of about two weeks in sea water, the copper content of the mussel tissue was back to normal—a fact quite in contrast to the situation with the barnacle.

TABLE XII

Changes in copper content of soft tissues of mussel during poisoning and recovery

Toxic: Cupric citrate
Test Animal: Mytilus edulis, 25 animals (5 cm. long) in each group
Date: August 19 to September 5, 1942
Basis: Copper content in milligrams per gram of dry weight of soft tissue

Exposure to toxic solution began August 19. The line marks the time when mussels were transferred to fresh sea water

Group	Concentration of Cu citrate mg. Cu/l.	No. of days in toxic	Content on indicated date							
			Aug. 20	Aug. 21	Aug. 22	Aug. 23	Aug. 24	Aug. 25	Aug. 26	Sept. 5
1	0.120	1	0.066	0.0196	—	—	—	—*	—	—
2a	0.082	1	—	0.0135	—	—	0.017	—	—	0.0085
2b	0.082	2	0.084	0.031	0.023	—	—	—	—	0.0077
3	0.049	3	0.0076	—	0.024	0.018	—	—	0.017	0.0100
4	0.027	5	0.0135	—	0.021	—	0.025	0.029	—	0.0130
Control	0	0	0.0109							

* Condition on August 25: Group 1—all dead
Group 2a—9 dead
Group 2b—10 dead
Group 3—3 dead
Group 4—4 dead

No further deaths to September 5.

In spite of the fact that after one day in sea water the copper content of the Group 1 mussels had been reduced at least to the amount reached by the mussels in the weaker solutions, all the animals in this group died within five days. Some irreparable damage had been done by the single day's exposure to the high concentration of the toxic. In the lower concentrations only three to four animals died despite exposures to the toxic for three to five times as long. It is possible that the mussels in the lower concentrations could eliminate copper from vital tissues as fast as it tended to enter.

Although the values obtained in this single experiment are somewhat irregular, two important differences are indicated by the results as compared with the results obtained with barnacles. At the same concentrations, the exposures which are lethal to mussels are considerably shorter than for barnacles. Similarly the mussels succumbed after accumulating amounts of copper in their tissues which were much lower than was the case with barnacles.

Tests on the Poisoning of Cyprids

During January, 1943, experiments were undertaken at Miami Beach, Florida, on the poisoning of barnacles in the cyprid stage. Especial interest centered on these observations because the cyprid is the stage in which the animal first attaches itself to the substratum. It is the opinion of many that once a barnacle becomes attached, it can be killed only with great difficulty and that even if it is killed, the shell does not drop off but remains firmly attached. Actually, attachment takes place in two steps: first, the attachment of the antennae of the cyprid, following which metamorphosis is begun; and second, the attachment of the base of the barnacle after metamorphosis has been completed.

Cyprids were obtained by suspending glass microscope slides in Biscayne Bay overnight. The cyprids were presumed to be those of *Balanus improvisus,* which is the commonest adult barnacle in the neighborhood. The slides were brought into the laboratory where the following details in the development of the cyprids were observed.

The cyprids are originally attached by their antennae. About 5 or 6 hours after attachment, the animal undergoes metamorphosis in the course of which the cyprid shell is moulted and the animal emerges as a more or less round body still adhering to the substratum by the original attachment which now appears as the center of the convex base of the animal.

As development proceeds the base of the animal, which was at first freely movable, tends to flatten and to be pressed against the substratum. About 24 hours after metamorphosis the base is completely flattened with relatively sharp edges. A pulsation of the central parts of the animal has begun by this time, and the operculum may open, but no cirri are extended. The base is not caused to move by the activity of the animal, as before, but any part of it, except the original central point of attachment, is easily dislodged by pressure with a needle.

After another 24 hours, the cirri may be extended and filter actively, and the main area of the base begins to adhere to the substratum. At first the base merely gives the impression of being sticky; later it becomes attached with sufficient firmness so that it cannot be dislodged without tearing the tissue. Not until the third day or later does hard material (presumably calcium carbonate) begin to appear in the base.

The attachment of the cyprid by its antennae takes place quickly, and the original attaching structure remains in existence at least until calcification begins. The attachment of the base of the newly metamorphosed barnacle is a slow process which provides only weak adhesion at first but which finally supplies a permanent and

TABLE XIII

Effect of different concentrations of cupric citrate in preventing the metamorphosis of barnacle cyprids attached to glass slides

Species: probably Balanus improvisus

Concentration mg. Cu/liter	Number of cyprids exposed	Number of cyprids which metamorphosed
116.	6	2 (moult incomplete)
58.	6	3 (moult incomplete)
23.	4	4
9.7	3	3
4.9	2	2
0.93	11	11
0.47	9	9
0.23	5	5
0.12	9	9

firmly cemented calcareous structure. Poisoning of the barnacle could theoretically be accomplished either in the attached cyprid stage or as a newly metamorphosed animal before the calcification of the base.

The susceptibility of the cyprid to poisoning was investigated by placing cyprids attached to glass slides in solutions of cupric citrate (Table XIII) and of mercuric chloride (Table XIV). In the case of the copper solutions, the cyprids metamorphosed successfully in concentrations as great as 23 mg. Cu/1 and solutions as strong as 116 mg. Cu/1 were only partially inhibitory. Concentrations about 100 times greater than those ordinarily tolerated by adult barnacles, therefore, were not capable of killing the cyprids before they completed their metamorphosis.

In the case of the mercury solutions, although an inhibitory effect was observed at a lower concentration (16.6 mg. Hg/liter) than for copper, much higher concentrations of the toxic were required to prevent metamorphosis than would ordinarily kill adult barnacles.

Failure to kill the cyprid may be due to an unusually high resistance of the animal to poison in this stage or to the relative shortness of the period between attachment and metamorphosis, or both. From these results it is probable that the metamorphosis of the attached cyprid cannot be stopped by any concentration of toxic which could practically be obtained from a paint.

TABLE XIV

Effect of different concentration of mercuric chloride in preventing the metamorphosis of barnacle cyprids attached to glass slides

Species: probably Balanus improvisus

Toxic solution mg. Hg/liter	Number of cyprids exposed	Number which metamorphosed
83.	5	0
16.6	6	3 (moult incomplete)
3.3	6	6
0.66	9	9
0.17	7	7
0.09	10	10

The susceptibility to poisoning of the newly metamorphosed barnacle was tested in a similar fashion by placing slides bearing animals in this stage in solutions of cupric citrate (Table XV). Much lower concentrations of copper were required to kill the newly metamorphosed barnacle than was necessary to prevent the cyprids from carrying out their metamorphosis. The relation between killing time and concentration is roughly of the same order of magnitude as observed for adult barnacles at Woods Hole. There is some indication, however, that the newly metamorphosed animals are slightly more resistant, as concentrations of 0.23 mg. Cu/1 to 0.47 mg. Cu/1 were required to kill in five days in contrast to concentrations of only 0.14 to 0.30 mg. Cu/1 for the older animals.

Although recently metamorphosed barnacles survived for several days in concentrations of cupric citrate of 0.12 mg. Cu/1 or lower, their development was very materially retarded. In the stronger solutions the base remained in the rounded condition, and in concentrations down to at least 0.20 mg. Cu/1 the base never became calcified nor rigidly cemented to the substratum, although it might become flattened and adhesive.

TABLE XV

Relation of killing time to concentration of cupric citrate in barnacles which had just completed metamorphosis

Species: probably Balanus improvisus

Concentration mg. Cu/liter	Killing time days
9.7	1
4.9	1–2
0.97	3
0.93	3–4
0.47	5
0.23	5
0.20	7
0.12	10

In a small number of tests reported subsequent to this investigation by Pyefinch and Mott (1944), free swimming cyprids of *Balanus balanoides* were killed in 24 hours by 0.5 to 1.0 p.p.m. copper from cupric sulphate. Metamorphosis was completed in concentrations up to 7 p.p.m. but after metamorphosis the barnacles were killed in 3 days by 0.5 p.p.m. Mercury from mercuric chloride was found to be more toxic than copper. These results agree very satisfactorily with ours.

At still lower concentrations of copper, in the present experiments, a complete change in the effect of the metal evidently comes about, for development was accelerated. Animals in the lowest concentration tested, namely 0.06 mg. Cu/1, reached the stage of active filtering with their cirri in less than 48 hours after metamorphosis, although the controls did not attain this stage until about 2 days later. It appears that a small amount of copper acted as a stimulant to development, and that larger amounts of copper retarded development even though they may be insufficient to kill the animals outright.

Discussion

Adult barnacles, and perhaps young stages also, can absorb ten to possibly one hundred times as much copper as their tissues normally contain without apparent injury. They can eliminate a certain amount of this material also. Therefore, when copper is used as a toxic in an antifouling paint, a substance is employed which can be taken up with impunity in relatively large quantities by the barnacle and to a lesser extent by the mussel. The animals can recover from the effects of this poison, to a certain extent at least, when again bathed by fresh sea water.

In some cases mussels which had received a lethal dose of poison remained in an apparent healthy condition for several days after being replaced in fresh sea water before dying. No such latent period was observed in the experiments with barnacles.

Possibly related to the facts just considered is the indication that the action of copper as a poison is not so much the direct destruction of some tissue or vital material in the barnacle as a general retardation of life processes. In the case of the adult barnacle, subjection to copper solutions causes a slowing and eventual cessation of the filtering activity of the cirri. In the case of the newly metamorphosed stages, not only is movement inhibited but development is seriously retarded as well. Much more satisfactory as a poison would be some substance which struck directly and irreversibly at some vital point in the animal and which could not be eliminated from the tissues. With such an ideal poison, barnacles which received only small doses, due to unavoidable dilution, would eventually be killed when a lethal amount of the material had accumulated. We have shown that with copper, sublethal doses may possibly stimulate development and certainly may allow subsequent recovery. Evidence that copper may stimulate the attachment of larvae has been reported by Prytherch (1934) for the oyster and by Miller (1946) for *Bugula*.

The relative vulnerability of the various steps in the attachment and growth of barnacles has been revealed by this investigation. The original idea that barnacles could be eliminated from a ship's hull only by preventing their initial attachment is partly right and partly wrong. As explained above, the attachment actually takes place in two steps. There is little promise of using poison successfully to prevent the first step, namely the attachment of the cyprid by its antennae, since this apparently takes place in a matter of minutes. However, we should not lose sight of the very important, but as yet unrealized, possibility of finding a substratum toward which the cyprid would display an avoiding reaction or to which the cement of the antennae would not adhere.[7]

Our tests have demonstrated the practical impossibility of preventing by poison the metamorphosis of the cyprid or of killing it during the process. This conclusion is substantiated by the results of Pyefinch and Mott (1944) and is in agreement with their statement: "Settlement and metamorphosis can take place on a paint in other respects anti-fouling though death of the barnacle occurs after metamorphosis." Similarly, at the other end of the life cycle, after the adult barnacle has attained any considerable size, it can be poisoned only with great difficulty for the reasons already discussed.

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[7] In certain tests under laboratory conditions, Pyefinch and Mott (1944) found that cyprids failed to settle in concentrations of copper as low as 0.03 p.p.m.

There remains, however, the possibility of effectively preventing the second step in the attachment process, namely the permanent cementing of the base of the newly metamorphosed animal to the substratum. Although a long exposure to copper or a high concentration is necessary to kill the barnacle outright at this stage, moderate concentrations of poison tend to retard development and possibly to prevent the formation of the calcareous base, or the cement for this base, with the result that the young barnacle never succeeds in establishing a firm attachment, and hence is eventually displaced. The newly metamorphosed stage, therefore, appears to be the most vulnerable to copper poisoning.

The indication is, then, that copper paints act by preventing attachment but do so chiefly during the second step of the process through interference with the final cementing of the base of the metamorphosed barnacle to its substratum.

SUMMARY

1. Direct tests were performed on the concentrations and exposures of a variety of metallic salts necessary to kill barnacles. The toxicities of mercury, cupric citrate, cupric tartrate, cupric salicylate, and cupric aminobenzoate were found to be slightly less than the toxicity of basic cupric carbonate. The toxicity of silver is about equal to that of basic cupric carbonate, but the toxicity of zinc is very much less.

2. The rate of killing of barnacles by cupric citrate is proportional to the concentration of the toxic over the range tested.

3. An extremely high concentration of copper or of mercury salts was necessary to prevent the metamorphosis of cyprids attached to glass plates. The results show the difficulty of preventing the *initial* attachment of cyprids, or their metamorphosis, by the use of copper paints.

4. Moderate concentrations of cupric citrate seriously retard the development of the newly metamorphosed barnacles and prevent the second step in attachment, namely, the formation of the cemented calcareous base.

5. Exposure of the newly metamorphosed barnacles to very low concentrations of cupric citrate accelerated development beyond that of the normal animals.

6. The soft tissues of adult barnacles normally contain a much higher concentration of copper than does sea water. When placed in solutions of cupric citrate, barnacles absorbed more than 100 times the normal copper content of the tissues. In no case were barnacles killed by the absorption of less than 0.19 mg. of copper per gram of dry weight—more than 10 times the normal content. In some cases barnacles which had absorbed 0.5 mg. to 1.09 mg./g. from toxic solutions revived when replaced in fresh sea water.

7. It was demonstrated that when replaced in fresh sea water, barnacles can eliminate from their tissues as much as two-thirds of the copper which has been absorbed from toxic solutions.

8. Mussels are more sensitive to poisoning by cupric citrate than barnacles. When exposed to copper solutions, mussels take up copper more rapidly than do barnacles, and when replaced in fresh sea water, they eliminate it from their tissues more rapidly and extensively. In many cases in which a considerable portion of the copper was eliminated, the mussels nevertheless succumbed subsequently.

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Over-water Refraction of 10-cm Electromagnetic Radiation

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ABSTRACT

A simple presentation is made of the optics involved in the nearly horizontal propagation of short radio waves above the spherical earth. The refraction produced by various types of atmospheric layers is discussed, especially the refraction in atmospheric layers close to a water surface and the resulting wide variation in possible range of communication between low-altitude terminals. A formula showing how the refractive index of air at radio wave lengths depends on moist-air variables is reproduced. A graph for the determination of potential refractive index is presented. As examples of over-water conditions, the vertical distributions of temperature, dew point, and potential refractive index are shown for two psychrometric ascents by airplane to 1000 feet.

THE PURPOSE of this paper is to present an introduction to a meteorological problem which was actively investigated by various groups during the recent war. More complete accounts are being prepared for publication elsewhere, particularly by the Radiation Laboratory, Massachusetts Institute of Technology.[2] Mention of the wartime developments has already been made by Sheppard (1946). A prewar study of atmospheric refraction of short-wave radiation has been presented by Friend (1945).

The refraction phenomena here described affect the band of wave lengths, briefly designated ''10-cm'' in the title, from about one centimeter up to several meters. At longer wave lengths these phenomena become negligible, and the ionosphere becomes important.

It is evident, from the new applications of short-wave communication and radar being developed, that there will be need for further meteorological study of low-level refraction.

1. Refractive Index of Air

The refractive index of air does not vary significantly with wave length over the entire range from about one centimeter up through all the radio bands. It depends on the air density and on the ratio of water-vapor concentration to absolute temperature, increasing with both of these. If the symbol n is used for refractive index, ρ for total density, q for specific humidity, and T for absolute temperature, and if A and B are dimensional constants, the basic relation is of the form (Friend, 1940, p. 352)

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[1] Contribution No. 361.

[2] Volume 13 of the *Radiation Laboratory Series*, to be published by McGraw-Hill Book Company, has the title *Propagation of short radio waves* and was written under the leadership of Donald E. Kerr. Chapter 3 of this book is "Meteorology of the refraction problem" by R. A. Craig, I. Katz, R. B. Montgomery, and P. J. Rubenstein.

$$n - 1 = A\rho(1 + Bq/T). \qquad (1)$$

The working equation adopted at the Radiation Laboratory[2] has pressure p and vapor pressure e as independent variables; it is

$$\left.\begin{aligned} n - 1 &= \frac{a}{T}\left(p + b\frac{e}{T}\right) \\ \text{where} \quad & \\ a = 79 \times 10^{-6}\,\mathrm{C\,mb^{-1}}, &\quad b = 4800\mathrm{C}. \end{aligned}\right\} \qquad (2)$$

In the atmosphere, refractive index tends to decrease upward due to the normal lapse of density, to decrease upward if there is a humidity lapse, and to decrease upward if there is a temperature inversion. An atmosphere of *homogeneous* air, namely, air in which potential temperature and water-vapor concentration are constant, forms a convenient standard and has a vertical distribution of refractive index not very different from that found under average atmospheric conditions. In homogeneous air the lapse rate of refractive index is positive, and its magnitude is about 0.8×10^{-6} per hundred feet. Rays directed nearly horizontally are therefore refracted downward, but the curvature is only about one sixth of the curvature of the earth (FIG. 1). The downward refraction allows rays to reach somewhat beyond the geometric horizon. Visible radiation is affected in the same manner; the sun and other objects are normally visible when they are slightly below the geometric horizon.

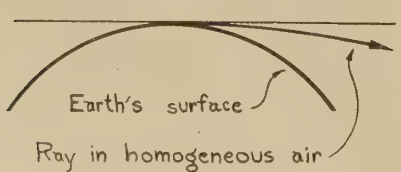

FIG. 1. Curvature of ray in homogenous air compared with curvature of earth's surface.

For radio waves, the refractive index in air is independent of wave length but depends very much on the water-vapor concentration. For light, it depends somewhat on wave length, but practically not at all on water vapor,[3] the second term on the right-hand side of (1) or (2) becoming negligible. The values for dry air given by the formula above are also approximately correct for light in air having any concentration of water vapor. In dry air, therefore, the refractive index is approximately the same for light and for radio waves. In air of constant water-vapor concentration the gradient of refractive index is approximately the same for both bands. In air of variable water-vapor concentration, however, the gradients may be entirely different. These qualitative relations may be useful if the refraction of radio waves is compared with such phenomena as mirage.

2. Propagation of Radiant Energy

The propagation of electromagnetic radiation is affected not only by refraction, as well as by partial reflection from ground and water surfaces, but also by absorption, scattering, and diffraction. If these last effects were non-existent, the feasibility of radio communication between two given points could be determined by tracing the rays (wave normals) emanating from one of the points; the density of these rays in the neighborhood of the other point would be an indication of the power received in communication between the two points. Although the method of ray tracing takes account of refraction only, it is nevertheless useful in providing a rough, preliminary guide to the energy distribution surrounding a given point of transmission.

The ray from the transmitter to the horizon is called the *tangent ray* (FIG. 2). Energy reaches the region above the tangent ray by direct radiation, but it penetrates the region below the tangent ray and beyond the point of tangency by the process of diffraction. The latter region is known as the *diffraction region.* The efficiency of the process of diffraction decreases rapidly as the wave length decreases. In the absence of diffraction, the tangent ray beyond the point of tangency would form a sharp boundary between the illuminated region and the earth's shadow.

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[3] See, for instance, Shaw (1930, p. 54).

Short-wave communication deep into the diffraction region is usually very difficult. Since the location of the tangent ray can vary widely due to changes in gradient of refractive index, it serves to explain why communication between two fixed points may be possible at some times and not at others. Likewise, the tangent ray drawn for the location of a radar set is a help toward determining which targets can be detected.

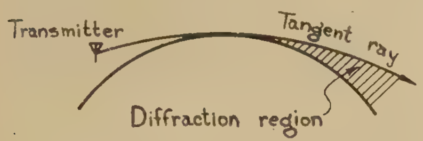

FIG. 2. Tangent ray in relation to earth's surface.

3. Types of Refracting Layers

If homogeneous air is regarded as a standard,[4] any layer in which the lapse rate of refractive index is less than the value found in homogeneous air may be called *substandard*, because its effect if any, is apt to be to increase the size of the shadow for a transmitter at a low elevation. A substandard layer occurs in hydrostatically stable air if there is an upward increase in water-vapor concentration sufficiently great to overbalance the effect of the upward increase in potential temperature. A second kind of substandard layer is that due to a superadiabatic temperature lapse rate accompanying constant water-vapor concentration. The second kind occurs in a shallow layer of air above warmer, dry ground.

The very great temperature lapse rate above a hot surface produces the visible effect of inferior mirage: on pavements and desert sand an image of the sky is formed by upward refraction and looks like a patch of water surface.[5] An actual inversion of refractive index, not merely a substandard layer, is required in order to produce inferior mirage; an inversion of refractive index for visible light accompanies an inversion of density, as may be seen from equation (1).

Any atmospheric layer in which the lapse rate of refractive index exceeds the value found in homogeneous air may be called *superstandard*, because its effect is apt to be to decrease the size of the shadow cast by the earth and, hence, to make communication between low-altitude terminals possible over ranges greater than those attainable in a homogeneous atmosphere. It can result from either an inversion of temperature (strictly, a lapse rate less than adiabatic) or a positive lapse of water-vapor concentration. Since the lapse of water-vapor concentration is normally positive, a temperature inversion is normally a superstandard layer. Although the substandard temperature inversion described above is sometimes observed, it is much less frequent. In visible wave lengths, since water vapor does not affect the refractive index, a temperature inversion is always a superstandard layer; under suitable conditions this layer results in looming, the phenomenon in which objects below the geometric horizon become unusually visible.

Two degrees of superstandard layer need to be distinguished. If the layer is only moderately superstandard, rays directed nearly horizontally have a curvature which, although greater than the curvature of rays in homogeneous air, is less than the curvature of the surface of the earth; this may be called a *type-1* superstandard layer. If the lapse rate of refractive index is sufficiently great, the rays' curvature exceeds the earth's curvature; this may be called a *type-2* superstandard layer. The critical refractive-index lapse rate separating the two types[6] is equal to the earth's curvature, or to the reciprocal of the radius, and therefore has the value 4.8×10^{-6} per hundred feet.

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[4] The "standard" vertical distribution defined in the book referred to above is somewhat different. It corresponds to a lapse rate of refractive index equal to about 1.2×10^{-6} (100 ft)$^{-1}$ instead of about 0.8×10^{-6} (100 ft)$^{-1}$.

[5] Regarding visible mirage see, for instance, Shaw (1930), Hurd (1937), or Humphreys, *Physics of the Air*, 3rd ed., p. 473.

[6] When the lapse rate of refractive index has this critical value, the "modified index of refraction" *M*, explained elsewhere (footnote 2), is constant by definition. An "inversion of modified index" or an "*M*-inversion" is the same as a type-2 superstandard layer.

If a type-2 superstandard layer exists next to the ground or sea surface, any horizontal ray in the layer does not reach the horizon but is refracted downward to the surface. If the surface is water, the ray is partially reflected, usually rather efficiently. By a process of successive upward reflections at the sea surface and downward refractions in the air, a ray is *trapped* between the surface and the level where it is horizontal. This process of successive deviations continues as far as the layer exists. For a transmitter located below the top of a type-2 layer, all rays are trapped which are emitted within a certain finite angle above and below the horizontal. The angle increases as the distance separating transmitter from top of layer increases, but it usually does not exceed half a degree. Those rays that are not trapped, however, remain in the layer for only a comparatively short path.

The concentration of rays within a type-2 superstandard layer represents a guiding of energy, enabling communication far beyond the normal horizon. In general, this effect increases in importance as wave length decreases. For a given type-2 layer, the operating range of a system with a wave length of 3 cm may be extended by a hundred miles or more, while the operation of an otherwise comparable system with a wave length of 2 m or 3 m may not be noticeably affected.

4. Conditions Close to a Water Surface

FIGURE 3 shows refractive index for a pressure of 1,000 mb as a function of temperature and vapor pressure; it was constructed from equation (2). The diagram includes lines of vapor pressure over two

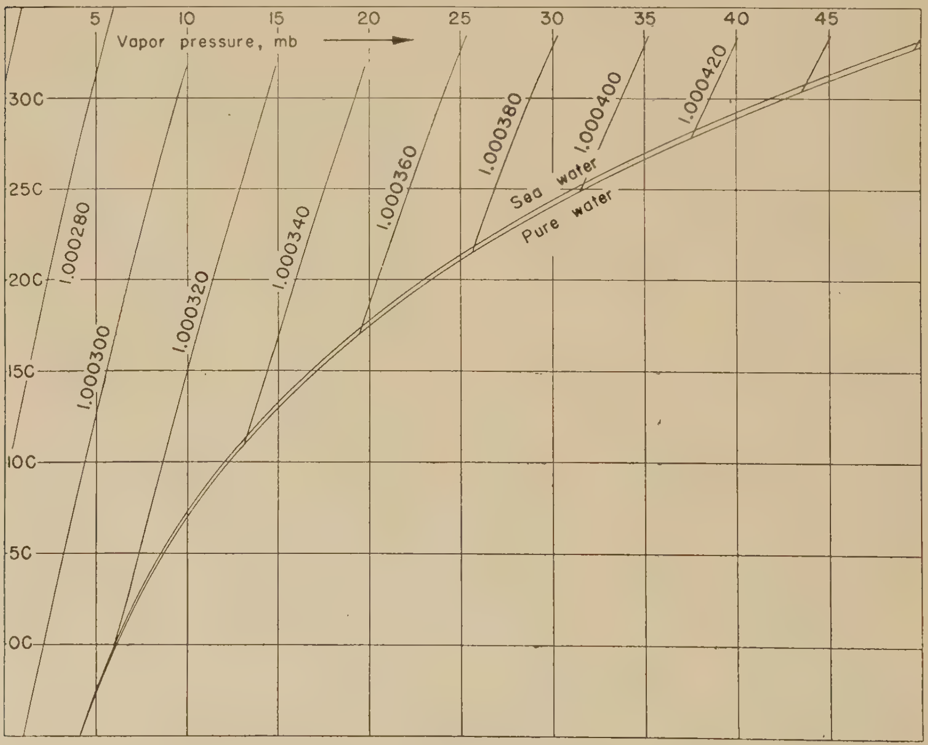

FIG. 3. Refractive index of air at a pressure of 1,000 mb. Vapor pressure over pure water and over sea water is shown by two bounding curves.

kinds of water surface.[7] The temperature of a water surface of given salinity determines both the air temperature and the vapor pressure at the surface; hence it determines the refractive index also. An important fact is that the refractive index of air in immediate contact with a water surface increases with temperature at all temperatures (except below −10C).

If the air a short distance above the air-water surface is potentially colder than the surface, its refractive index is seen to be less than the refractive index at the surface. In this case of *cold air over warm water* the surface layer of air is therefore always superstandard.

In the case of *warm air over cold water* the surface layer of air may be either superstandard or substandard depending on the humidity of the air. Only if the upward increase in potential temperature is counterbalanced by a sufficient inversion of vapor pressure can the layer be substandard. The temperature of the air-water surface determines a point on the diagram in Fig. 3. An isopleth of refractive index extends diagonally upward from this point. If the point representing the air a short distance above the surface lies to the left of this line, the surface layer is superstandard; if it lies to the right, the surface layer is substandard.

Above a water surface a lapse of vapor pressure is more frequent than an inversion of vapor pressure. Therefore, for radio waves, the surface layer of air is more frequently superstandard than substandard. Furthermore, close to the surface the vapor-pressure lapse is usually large, giving type-2 superstandard conditions. The conditions affecting visible radiation are usually less pronounced: since humidity gradients are unimportant, abnormal refraction is caused by temperature gradients only, and large temperature gradients above a water surface are less frequent than large humidity gradients.

A diagram having temperature and vapor pressure as coordinates (Fig. 3) is useful, in the same way as is the Rossby diagram, as a *characteristic diagram.* Since Taylor (1917) used it in discussing mixing processes and fog formation, a diagram with these particular coordinates may suitably be called the *Taylor characteristic diagram.* If over-water soundings are plotted on it, such a diagram aids in their interpretation. Another application is that it serves for plotting rapidly repeated observations at a fixed point; the resulting scatter diagram shows the relation between the fluctuations in temperature and those in vapor pressure.[8]

5. *Potential Refractive Index, n_p*

The vertical distributions of temperature, humidity, and refractive index in the lower atmosphere over land or water are greatly influenced by turbulent mixing. For this reason, as well as others, it is sometimes convenient to express each of the three properties by means of a quantity which is (a) conservative during adiabatic changes of pressure and which is (b) equal, in a mixture, to the average by mass of its values in the ingredients. Each such quantity is, consequently, (c) constant throughout homogeneous air.

These desiderata are satisfied by potential temperature and by water-vapor concentration. The vapor pressure of any mixture is equal to the mean by mass of the vapor pressures of the ingredients, if all are at the same total pressure; consequently both desiderata are satisfied by potential vapor pressure. When a chart like Fig. 3 is used as a characteristic diagram, the two variables plotted on it should be potential temperature and potential vapor pressure.

Potential vapor pressure is defined in the same way as potential temperature. The *potential vapor pressure* of a sample of air is the vapor pressure that would result if the sample were changed adiabatically and without change in composition) to a standard pressure. Likewise, the *potential refractive index,* n_p, may be defined as the refractive index a substance would have if changed adiabatically to a standard pressure. It satisfies the desiderata described above.

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[7] The values of vapor pressure over water above freezing and over ice are from the "Smithsonian meteorological tables" (1931). Values for supercooled water are given by Harrison (1934). The vapor pressure over sea water of salinity 35 per mille is 98.12 per cent of its value over pure water (Sverdrup, Johnson, and Fleming, 1942, p. 115).

[8] The author is preparing a paper explaining some uses of the Taylor characteristic diagram.

Potential refractive index, like potential temperature and potential vapor pressure, is constant in homogeneous air. It increases upward in a substandard layer and decreases upward in a superstandard layer. In a type-2 superstandard layer the lapse rate of potential refractive index exceeds about 4.0×10^{-6} per hundred feet (the critical lapse rate of refractive index less the lapse rate of refractive index in homogeneous air).[9]

In work with measurements over the ocean it is not convenient to compute potential values by use of a fixed standard pressure such as 1,000 mb, because such values would not be directly comparable with actual values at the surface. For instance, although at the surface the water temperature is the same as the air temperature, it is not the same as the potential temperature of the air referred to 1,000 mb unless the surface pressure happens to be exactly 1,000 mb; there is ordinarily a discrepancy of a degree or two.

Sea-level pressure, therefore, is chosen as the standard pressure for potential temperature and potential vapor pressure in what follows. If temperature or vapor pressure is measured at a known height above sea level, the potential value is obtained by adding to the measured value the product height times lapse rate, in homogeneous air, of temperature or of vapor pressure.[10]

Refractive index and potential refractive index depend on sea-level pressure. This variable may, however, be eliminated for practical purposes, because the vertical gradient is of primary concern rather than the absolute value. For potential refractive index one may use the refractive index of air having temperature equal to the potential temperature, vapor pressure equal to the potential vapor pressure, and pressure equal to 1,000 mb. The formula for it, if θ_{sl} is potential temperature and e_{sl} is potential vapor pressure (both in terms of sea-level pressure), is

$$n_p - 1 = \left(\frac{a}{\theta_{sl}} 1000 \text{ mb} + b\frac{e_{sl}}{\theta_{sl}}\right). \quad (3)$$

Numerical values of this form of potential refractive index may be read directly from a diagram like that in Fig. 3 by entering with potential temperature and potential vapor pressure.

6. *Examples*

During 1943, 1944, and 1945 the Radiation Laboratory, with the collaboration of various Federal departments, carried out both radio-transmission measurements[11] and low-level atmospheric soundings of temperature and wet-bulb temperature. The most successful soundings were made from airplanes; the speed of the airplane has been allowed for in reducing the observations to true temperature and dew point of the undisturbed air. Two examples are shown in Figs. 4 and 5.

In the first example (Fig. 4) the temperature of the water is intermediate between the temperature and the dew point of the air. Consequently, eddy diffusion carries heat downward to the water surface and carries the water vapor upward that is evaporated from the surface. The inversion of temperature and the large lapse of dew point in the lowest few hundred feet makes the layer superstandard. In the lowest 150 ft the lapse rate of potential refractive index exceeds 4.0×10^{-6} per hundred feet and is therefore type-2 superstandard. The layer from 150 ft to 400 ft is type-1 superstandard. Above 400 ft the air is approximately homogeneous.

Experience has shown that the results of psychrometric observations may conveniently be represented, in vertical distribution, by temperature and dew point. This pair can be shown on the same graph, as in Figs. 4 and 5, and so can the water temperature. At the water surface the temperature is the same for air and water. If the water is

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[9] In Figs. 4 and 5 the scales of height and potential refractive index are so related that a line with slope minus one separates type-1 from type-2 lapse rates of potential refractive index.

[10] This method is not strictly precise because of the density difference between the fictitiously displaced parcel and the environment. For low-level soundings, however, the actual discrepancy is insignificant.

[11] See chapter 4 of the book referred to above (footnote 2).

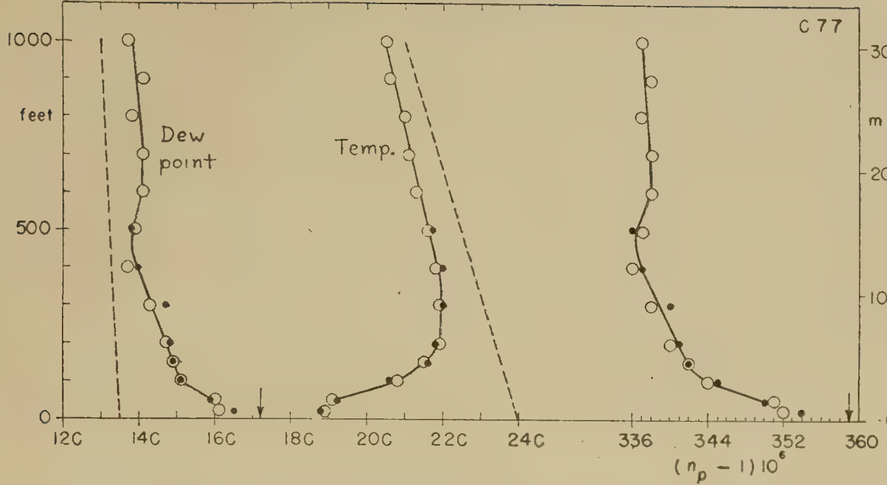

FIG. 4. Over-water airplane sounding number C77 on 26 July 1944 at 42°31′N, 70° 36′W, 5 miles southeast of Cape Ann, Massachusetts. Large open circles represent first ascent at 09^h57^m–10^h07^m, small solid circles represent repeat ascent at 10^h09^m–10^h16^m (time meridian 60°W). The dashed lines show the vertical variations of dew point and temperature in homogeneous air. Arrows indicate possible values at the air-water boundary. Surface wind was observed to be SSW force 1 Beaufort. Water temperature of 17–19C was measured from boat a few miles away.

fresh, the dew point at the surface coincides exactly with the surface temperature. At a surface of salt water the dew point is about 0.3C lower than the temperature, a difference which is so small as to be unimportant in most cases. Each curve drawn in the illustrations is to be extended in imagination from 20 ft, the lowest point of the sounding, down to the arrow representing the surface value. The arrow for water temperature is the termination of the curve for temperature; for practical purposes, it is the termination of the curve for dew point also.

In the second example (FIG. 5) the water temperature is lower than the dew point, a rarer occurrence than the situation in the first example. Eddy diffusion carries both heat and water vapor downward, and water vapor condenses on the sea surface. The distribution of potential refractive index below 150 ft is mostly substandard.

Cross sections based on a few others of the many Radiation Laboratory soundings have already been published by Craig, Katz, and Harney (1945). Nearly a hundred more soundings have been prepared for publication and are expected to appear in the near future.[12]

7. *Summary of Over-water Conditions*

When the air is potentially warmer than the water, a group of phenomena of widely varying effect may occur: Anomalous distributions of refractive index may extend several hundred feet up from the surface. While superstandard layers are more frequent, substandard layers occur at times, and both may exist simultaneously at different heights. Because the anomalous layers are so thick, they affect the maximum range attainable by use of 10-cm radiation between two points at low elevation over the ocean. Conditions of the sort shown in FIGS. 4 and 5 have been observed to have a marked favorable and unfavorable effect, respectively, on the transmission between two such points.

When the air is potentially colder than the water, a different phenomenon occurs,

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[12] Some of these are included in the book referred to above (footnote 2). Subsequent to the preparation of the present paper, a large group of soundings have been published by Craig (1946).

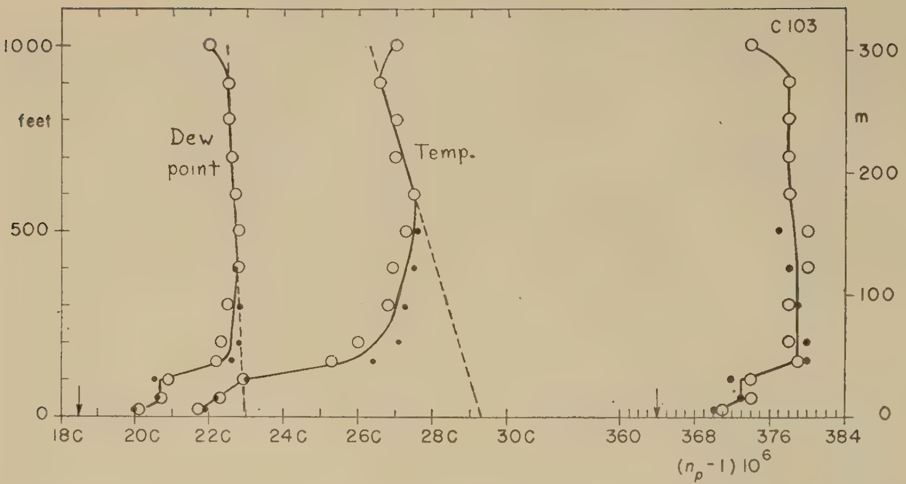

Fig. 5. Over-water airplane sounding number C103 on 14 August 1944 at 42°08½′N, 70°16′W, 5 miles north of Race Point, Cape Cod, Massachusetts. Large open circles represent first ascent at 10^h58^m–11^h08^m, small solid circles represent repeat ascent at 11^h15^m–11^h20^m. Surface wind was observed to be SSW force 3 Beaufort. Water temperature of 21C measured at same time on beach at Race Point.

not included in the examples. The superadiabatic temperature lapse rate near the water surface is accompanied by a much greater lapse rate of dew point (so that both heat and water vapor are carried upward by eddy diffusion). A markedly superstandard surface layer always results. It is, however, comparatively shallow. The thickness of the type-2 superstandard surface layer may be between 5 ft and 50 ft and the noticeably superadiabatic temperature lapse rate does not extend much above this layer. Above the shallow superadiabatic and superstandard surface layer the air is nearly homogeneous, because it is continually mixed by convection due to the warm, underlying surface. When the potential temperature of the air is close to the water temperature and at least a light breeze is blowing, conditions are not very different from those just described. The superstandard surface layer in either case may increase the radio range if the layer is both "strong" enough and thick enough and if the wave length of the radiation is sufficiently short and transmitter and receiver are in the layer or not far above; otherwise it may be quite ineffective.

Acknowledgment.—The author is grateful to Mr. Donald E. Kerr, Research Laboratory of Electronics, Massachusetts Institute of Technology, for certain information included in this article and for his careful examination of the manuscript.

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FORAMINIFERA OF THREE SUBMARINE CORES FROM THE TYRRHENIAN SEA

BY

FRED B. PHLEGER, JR.

WITH A FOREWORD BY

HANS PETTERSSON

COMMUNICATED FEBRUARY 10, 1947

GÖTEBORG 1947
ELANDERS BOKTRYCKERI AKTIEBOLAG

FOREWORD

The recent progress made in the technique of sediment coring, especially by Kullenberg's »piston-corer» (1), allowing of taking undisturbed sediment cores exceeding 20 metres in length, has made the call for methods of dating such cores imperative. In chronological studies of geological formations on the continents radioactive age-determinations, using the known rate at which helium and radio-lead are produced at the disintegration of the ancestral elements uranium and thorium, have afforded means of measuring the age in tens or in hundreds of millions of years. With more recent formations the enormously slow rate at which these elements disintegrate, uranium to 50 % in 4 500 million years, thorium to 50 % in 13 000 million years, makes the method inaccurate or even quite useless when the age is less than a few million years. For this reason alone no help can be expected from the uranium/thorium: lead/helium relationship in submarine chronology as applied to the ocean deposits. On the other hand the precipitation of ionium together with ferric hydroxide going on in seawater, suggested by the present author in an earlier paper (2) as an explanation for the deficiency of radium in seawater as compared with its uranium content (which, incidentally, gives an explanation for the high radium content in many deep-sea deposits (3)) has already proved useful in the dating of long sediment cores by measurements of their content of ionium-supported radium in different levels (4). It seems reasonable to expect that in localities where the processes of precipitation and of sedimentation have remained in constant proportions for a sufficient length of time radioactive age-determinations will be useful to submarine geology.

However, since the half-period of ionium is only a little more than 80 000 years, strata deposited a quarter of one million years ago will only contain about one eighth of their original content of ionium, as represented by the uppermost surface layer, and hence also of radium in equilibrium with its parent element. It is, therefore, to be expected that much older strata will hold radium only in quantities too small for accurate measurements.[1]) It is of interest here to remark that unsupported radium too, disintegrating to 50 % already within 17 centuries, may, in some cases, give clues for determining the age of suboceanic formations. In an earlier contribution to this series the author has shown, that the radium entering together with the manganese into the so-called manganese nodules found in great depths, has afforded means for determining their rate of radial growth to about 1 millimetre in 1 000 years. If we compare the immensely slow uranium and thorium decay to the hour hand of the radioactive clock, we may compare the much more rapid ionium decay to the hand showing the minutes of geological time, and the still more rapid radium decay to the hand showing the seconds. Only the two latter hands seem to come in useful in suboceanic chronology.

There are, however, also other means available for such chronological studies. One of them is offered by the presence of volcanic ash-layers in the sediments, due to vast eruptions of the explosive type spreading their finest ash particles over enormous areas of the ocean surface. With the help of such ash-layers from historic eruptions, like that of the Tambora on Soembawa (1815), present in cores raised during the Dutch Snellius expedition, Miss NEEB (5) has been able to date the uppermost parts of several cores. It appears as if the numerous ash-layers found in cores from the Tyrrhenian Sea during the recent »Skagerak» expedition (6) may afford clues for similarly dating the uppermost layers also in the western Mediterranean. With midoceanic cores containing layers of volcanic ash, like those raised by Dr C. S. PIGGOT by means of his ingenious explosive core-sampler (7) from the bottom of the North Atlantic, at least a relative dating by identifying the ash-layer from the same eruption in different cores may become feasible.

The beautiful pollen analysis developed in Sweden especially by von POST and his co-workers has proved to be of great service to post-glacial chronology. A preliminary analysis of the pollen present in the three cores from the Tyrrhenian Sea has proved them to be surprisingly rich in pollen grains although, mainly for lack of pollen-analytical data from the surrounding countries, no attempt at any dating has so far been feasible. It remains to be seen in how far the pollen grains present in cores from the open oceans, which we hope to raise during the planned Swedish deep-sea expedition with the »Albatross», will be found to contain pollen grains of recognizable types in numbers sufficiently large for an analysis.

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[1]) The initial increase in radium immediately below the surface due to its production from the precipitated ionium, and also the residual activity due to the small quantity of uranium-supported radium present also in much deeper strata, are here disregarded.

A fourth though highly hypothetical line of approach to suboceanic chronology seems to be afforded by quantitative determinations of the number of »cosmic spherules» (frozen drops of meteoritic iron found by Sir JOHN MURRAY in the deepest deposits) in different layers of the same core. If paralell variations with increasing age of the strata in the number of such cosmic spherules should become apparent in cores from different localities, a kind of relative age determination may become possible, quite apart from the interesting information such variations, if found to be universal, would throw on the past cosmic history of the solar system.

The fifth and perhaps most promising line of approach to suboceanic chronology lies in analysing the remains of planktonic organisms, especially the calcareous shells from pelagic foraminifera, present in the sediment. The composition of surface plankton is known to be influenced by the surface temperature. Thus thermophile species like *Globigerinoides sacculifera* will be reduced in numbers or even disappear altogether during spells of colder climate, reappearing again with a rise in water temperatures, when the ice-age has passed and the climate improves. By analysing the foraminiferal shells present in different layers of deep-sea cores raised from the bottom of the equatorial part of the Atlantic Ocean during the »Meteor Expedition» W. SCHOTT (9) was able to distinguish between layers of glacial and postglacial age, and thus date the limit between the two layers at about 20 000 years back in time.

It appeared highly desirable to the present author to have samples, taken from different levels of the cores from the Tyrrhenian Sea, analysed by an expert on foraminifera with the purpose of ascertaining whether there are in these cores any signs of climatic changes. Thanks to the kind intervention of Dr MARY SEARS of Woods Hole Oceanographic Institution it was the good fortune of the author to interest Dr FRED PHLEGER of Amherst College and Woods Hole in the problem. In spite of the strictly limited time Dr PHLEGER kindly undertook the analysis of 28 samples from the three cores. His results, presented in the following paper, are extremely interesting and appear to give reasonable hopes that an approximate dating of these as well as of other cores from the Mediterranean will be feasible, although the amount of work required for a complete analysis of the total length of these cores, viz. 150 metres, appears rather formidable.

Oceanografiska Institutet February 1947

Hans Pettersson.

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Introduction.

The Foraminifera contained in 28 samples from three cores taken from the Tyrrhenian Sea have been examined. The locations and descriptions of the cores are given elsewhere in this journal. The positions within the cores of the samples for Foraminifera are listed in Table 1. This core material was furnished to the writer by Professor HANS PETTERSSON of the Oceanografiska Institutet of Göteborg. It has been a great privilege to study these interesting faunas obtained by the new submarine coring tube, and the writer expresses his sincere appreciation to Professor PETTERSSON.

The purpose of this study is to determine the vertical variations in foraminiferal faunas, if any, which occur in the submarine sections represented in these three cores, and to present suggested interpretations. This is not intended to be a complete faunal study, but is a vertical faunal reconnaissance. These are only three of several long submarine cores which have recently been obtained by the new KULLENBERG coring tube from the Mediterranean Sea. The present report suggests how a complete study of the Foraminifera of these and other submarine cores from the Mediterranean may be done, and the results to be expected from such a study are indicated.

Method of Study.

The writer does not know the methods used in sampling the cores, but it is assumed that the samples were taken more or less at random. All samples were of the same approximate size, but no attempt was made to measure them. It is assumed that reasonable precaution had been taken to prevent faunal contamination of the samples, and especially that they had been carefully trimmed after sampling. There is some suggestion of mixing of faunas but there is no good evidence for this.

The samples were prepared by washing out the mud fractions through a brass sieve having a size of opening of 105 microns. The coarse fractions of the samples were so small that it was not necessary to concentrate the Foraminifera by flotation. The faunas have been studied quantitatively, as described previously (Phleger, 1941; Phleger and Hamilton, 1946). The samples are quartered so that not more than approximately 500 specimens are counted in each sample. This is considered to give a representative count of all but the very rare species in any sample. The accuracy of this method is certainly as high as the accuracy of the original sampling of the bottom.

The occurence of species within the faunas is reported on a percentage basis in which the pelagic and the benthonic fractions are considered separately (see Table 2). Each sample thus has the pelagic species listed as comprising 100 % and the benthonic species as 100 %, giving a total of 200 % for each sample. The reason for thus handling the data is that the benthonic and the pelagic fractions of any foraminiferal fauna represent two different phases of the marine environment.

The Foraminifera.

The writer has had little first-hand acquaintance with the Mediterranean foraminiferal faunas. Almost all of the pelagic species which occur in these are common to the North Atlantic and elsewhere, however, and many of the benthonic species are also widely distributed. No attempt has been made to identify the benthonic species which are not familiar to the writer, but these constitute such a small percentage of the faunas that they can be neglected. The faunas in these cores are pelagic, with benthonic forms constituting only a very minor fraction of any of the samples.

Interpretation of the water temperature conditions indicated by the faunas in the cores is based upon inadequate knowledge of the ecology of Foraminifera. We do know something of the geographic distribution of various species and assemblages and it is generally assumed that they are related principally to water temperatures. This information on distribution is almost entirely qualitative. The principal bases of interpretation of the core assemblages are suggested below.

Identification of many of the species of the Globigerinidae is somewhat uncertain, especially of small and presumably juvenile specimens. Adult specimens generally are not difficult to identify but there are many apparent intergradations between species. Many small specimens have been identified as *Globigerina bulloides* which may be young specimens of some other globigerinids. Also, it is not possible to say with certainty whether some small specimens are *G. pachyderma* or are small (young?) specimens of *G. inflata*. In the present samples it is also possible that some specimens of *Globigerinoides rubra* are incorrectly identified as that species. Despite these difficulties it is believed that errors in identification are of little quantitative significance in dealing with a large number of specimens.

Globigerina bulloides apparently is more or less universal in distribution. It appears to constitute a major precentage of a fauna only under conditions where water temperatures are not in the tropical, or possibly even warm-temperate, range. It is one of the most abundant species in sub-Arctic and sub-Antarctic areas, being the only pelagic foraminifer present in some shallow-water areas in these latitudes. Also it is reported in some abundance in relatively cool-water areas within the tropics, such as in the Guinea Current. It is considered to indicate »cool-water» conditions where it is present in considerable quantity, and if »warm-water» forms are rare or generally absent. *G. inflata* in abundance is believed to be indicative of warmer water than *G. bulloides*, both from its distribution in the present-day fauna and also its occurrence in submarine core faunas in the western North Atlantic. It is observed that an increase in abundance of *G. bulloides* is accompanied by a decrease in abundance of *G. inflata*, and *vice versa*. *G. pachyderma* is typical of Arctic and Antarctic regions, but does occur in mid-latitudes in some places in the western North Atlantic. It is not characteristic of the modern Mediterranean fauna. Specimens apparently belonging to *G. dubia*, previously known from the North Atlantic, have been found in significant quantity in some samples. The writer suggests that *G. dubia* may be characteristic of a moderately warm-water assemblage.

Globigerinoides rubra has been found in some abundance in most of the samples. The significance of this species is uncertain, but it may be able to tolerate rather large temperature ranges. There is evidence that it lives at considerable depth along with *Globigerina bulloides* in the North Atlantic (PHLEGER 1945). *Globigerinoides sacculifera* apparently is characteristic of low and mid-latitudes, and its presence in significant quantity is characteristic of many warm-water faunas. *Globigerinella aequilateris* also is characteristic of warm water.

Globorotalia truncatulinoides and *G. hirsuta* are characteristic of warm water. *G. acitula* is a cold-water form, according to its known distribution. It is very doubtful, whether it is living in the Mediterranean at the present time, although occasional specimens may be introduced from the North Atlantic. *Orbulina universa* and *Spheroidina bulloides* are characteristic of warm water.

Benthonic forms constitute only a very minor percentage of these oceanic, deep-water faunas, and their ecologic significance is difficult to understand. They have not been used in the interpretation of the core faunas, except in a very minor way. *Cassidulina laevigata* and *C. subglobosa* in relative abundance frequently accompany a cold-water pelagic assemblage, and the significance of this is difficult to understand at the present time.

The Core Faunas.

Vertical faunal differences are present in these three cores, and they are interpreted as representing differences in water temperatures when the different faunas were being accumulated. A summary of the writer's interpretation is presented graphically in Figure 1. In this figure the fauna in each sample is represented as being of »warm» or »cold» type, and the distance of its position from the center line indicates in a general way how far it tends toward the warm or cold extremes. The extreme positions of any of the samples would indicate perhaps very warm temperate faunas in the left-hand column and sub-Arctic or Arctic faunas in the right-hand column. These interpretations are very largely based upon the writer's experience with core Foraminifera from the western North Atlantic and upon the distribution of the modern faunas.

Core 13. The top sample (1301) furnished to the writer contains only 23 specimens belonging to *Globigerina bulloides* and *Globorotalia scitula*. It appears quite probable that this pelagic fauna is not characteristic of the Tyrrhenian Sea at the present time. This is also indicated by the fact that it is quite different from the faunas in cores 15 and 16. Sample 1301 may represent either contamination

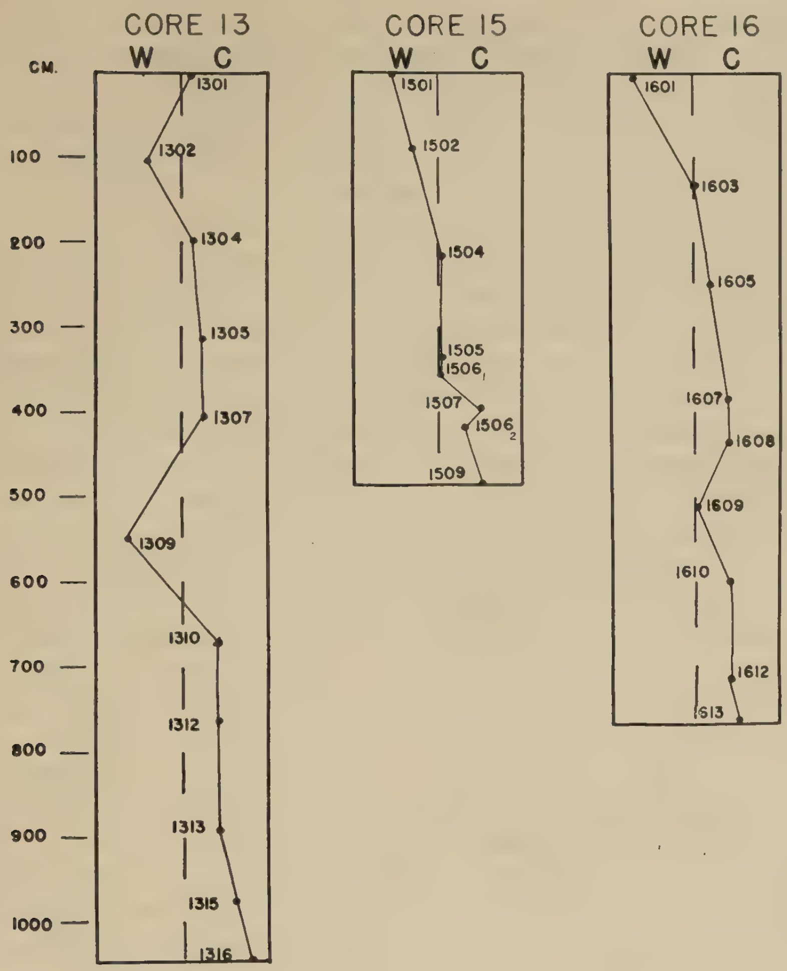

Figure 1. Approximate relative temperatures represented by the Foraminifera in the cores.

from an unknown source or unusual conditions which cannot be explained with the information at hand.

Sample 1302, at 102,5 to 103.0 cm., contains a moderately warm-water fauna which is very similar to the faunas at the tops of cores 15 and 16. Below this is a fauna representing colder conditions, containing high percentages of *Globigerina bulloides* and *G. pachyderma* and insignificant occurrences of warm-water species. This cold-water fauna, probably representing cool-temperate to sub-Arctic conditions, occurs from sample 1304 at 198 cm. to sample 1307 at 409 cm. It is interesting to note that *Cassidulina laevigata* also is significant in this zone, although it is not present in samples taken immediately above and below. *Orbulina universa*, a warm-water species, is present in this zone, but this is here interpreted as representing contamination from sample 1309 beneath or from some other source. *O. universa* is an erratic species in this assemblage.

Sample 1309, at 554 to 554.0 cm., contains a warm-water fauna which has a generally warmer water aspect than sample 1302. This is indicated by the relatively low percentage of *Globigerina bulloides* and *G. pachyderma*, the relatively high percentage of *Globigerinoides rubra*, *Orbulina universa*, and the presence of *Globigerina dubia*, *Globigerinella aequilateris*, and *Globorotalis truncatulinoides*.

Sample 1310, at 670.5 cm. to 672.5 cm., contains a coldwater fauna which is dominated by *Globigerina bulloides*, *G. pachyderma* and *Globorotalia scitula*. Essentially the same fauna continues to the bottom of the core at 1 045.5 cm. It is believed that sample 1316 represents colder conditions that any of the above samples. This is based upon the small number of specimens, consisting mostly of *Globigerina bulloides* and *G. pachyderma*.

Core 15. Sample 1501, at the top of the core, contains a sparse fauna which is warm-temperate. 1502, at 89.5 to 90 cm., also has a warm-temperate fauna, but the high percentage of *Globigerina pachyderma* suggests that it may indicate somewhat cooler conditions unless faunal contamination has occurred. Samples 1504 to 1506, from 214 to 358 cm., appear to represent intermediate water temperatures tending to be somewhat colder than warmer. 1507, 1506_2, and 1509, extending from 393 to 483.5 cm., all contain cold-water faunas dominated by *Globigerina bulloides*, *G. pachyderma*, and *Globorotalia scitula*. *Globigerinoides rubra* also occurs in significant percentages in these lower three samples, but this is not believed to be significant.

Core 16. Sample 1601, at the top of the core, contains the most characteristic warm-temperate fauna of any of the samples which were examined. 1603 contains a transitional fauna, characterized by an abundance of *Globigerina pachyderma*, and an increase in *G. bulloides* and *Globorotalia scitula*. Samples 1605 to 1608, from 251 to 435.5 cm., are cold-water; 1605 may indicate slightly less cold water conditions than 1607 and 1608. There is an indication of slightly warmer conditions in the fauna of sample 1609, at 512 to

514 cm., mainly in the increase in percentage of *Globigerina inflata;* however, this sample is believed to represent essentially cool water conditions. Sample 1610, at 599.0 to 600 cm., contains a cold-water fauna, and this continues to the bottom of the core at 770 cm.

Discussion.

The evidence gained from the Foraminifera contained in the few samples which have been examined from these three cores indicates that cooler water conditions than at present obtained during a large part of the time represented by the length of the cores. These cooler conditions are undoubtedly to be correlated with climatic changes on land. Similar faunal variations in the North Atlantic have been correlated with climatic changes on land, and the cold-water faunas in the lower parts of the cores from the Tyrrhenian Sea may represent the last phases of Pleistocene time. Similar faunal variations in the North Atlantic have been correlated with Pleistocene climatic variations by CUSHMAN and HENBEST (1940) and PHLEGER (1939, 1941).

The modern fauna occurs in the upper 100 to 150 cm. of the cores, and below this most of the samples contain a fauna at present restricted to very cool-temperate or sub-Arctic areas.

Core 13, the longest of the three, contains two sub-Arctic faunas separated by a warm-temperate fauna at a depth of about 550 cm. These cold-water faunas possibly may be correlated with separate advances of the last Pleistocene ice sheet on land, as suggested by PHLEGER and HAMILTON (1946). There is also a suggestion of an interglacial, or interstadial, in sample 1609 in core 16.

It is desirable that there be further study of the Foraminifera from these and the other cores which have been taken from the Mediterranean before definite conclusions can be made from the faunal variations. The writer ventures to suggest how these studies should be done, based largely on experience obtained in studying similar materials from the western North Atlantic.

It is suggested that all the cores be studied by the continuous sampling method described by PHLEGER and HAMILTON (1946). This is a detailed method of sampling in which the entire length of each core is divided into small samples which are separately analyzed. It is believed that this method is the only reliable one inasmuch as it clearly brings out all faunal variations. In the present cores there is no certainty that all significant faunal variations which are present are indicated by the samples.

It is desirable that the sampling of the cores and the preparation of the samples be done or supervised by the investigator who studies the Foraminifera. Recent Foraminiferal faunas become contaminated easily because of the small size of the specimens, and all reasonable precautions must be taken to avoid contamination. The structure of each core should be studied for possible evidences of mixing. In any submarine coring the material is mixed on the outside of the core, and this must be trimmed off. All cut surfaces also must be trimmed, and the samples must be handled with great care after collection. There is considerable evidence that some of the samples studied for the present report may have been contaminated. It is always difficult to be certain of contamination, however, because the sample may contain a transition fauna. It is essential that reasonable precautions be taken to avoid any artificial faunal mixing.

In handling a long submarine core aboard ship and in transporting it there is always the danger that the topmost sample will be lost or mixed. This is because it is generally in a fluid condition, and usually it is not possible to keep a core in a vertical position. The top sample contains the modern fauna, which is essential as a reference for interpretation of the lower faunas in the core. It is suggested that a bottom sample be taken at the position of each core to obtain the fauna which occurs at the surface of the bottom.

It is believed that further study of submarine core Foraminifera from a sufficient number of submarine cores from the Mediterranean will give considerable information on the variations of marine climate during the recent geologic past in that area.

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Contribution No. 364, Woods Hole Oceanographic Institution.

Table 1. *Positions of the samples within the cores.*

Core 13.

Location: 40° 14′ N. Lat.
12° 19′ E. Long.
Depth: 3 620 meters.

1301	3—5 cm. below surface
1302	104—104.5
1304	198—203
1305	315.5—316
1307	404—409
1309	554—554.5
1310	670.5—672.5
1312	760.5—761
1313	891.5—893.5
1315	975.5—977.5
1316	1 045—1 045.5

Core 15.

Location: 40° 36′ N. Lat.
13° 20′ E. Long.
Depth: 1 994 meters.

1501	1.5—2 cm.
1502_1	89.5—90
1502_2	135.5—136
1504	214—214.5
1505	334—334.5
1506_1	357.5—358
1506_2	418.5—49
1507	393—393.5
1509	483—483.5

Core 16.

Location: 40° 31.5′ N. Lat.
13° 10′ E. Long.
Depth: 2 716 meters.

1601	Within 10 cm. from surface, mixed up with ash.
1603	133.5—134 cm.
1605	251—253
1609	512—514
1612	716.5
1613	770
1608	434.5—435.5
1607	383.5—384
1610	599.5—600

Table 2. *Percentage frequencies of the Foraminifera in the samples.*

Sample	Core 13									
	1301	1302	1304	1305	1307	1309	1310	1312	1315	1316
Total No. of Specimens	23	66	2 130	558	1 872	5 243	5 325	1 764	1 488	22
Pelagic Species %										
Globigerina bulloides	80	52	57	43	63	30	74	36	51	31
G. inflata	—	19	5	2	2	23	2	0.3	—	—
G. pachyderma	—	5	27	27	14	7	5	14	3	52
G. dubia	—	1	—	—	0.3	2	—	14	—	—
Globigerinoides rubra	—	17	22	18	16	32	5 326	22	16	9
G. sacculifera	—	—	—	—	—	—	—	—	—	—
Globigerinella aequilateris	—	—	—	—	—	0.1	—	—	—	—
Globorotalia truncatulinoides	—	1	0.5	—	—	0.3	—	—	—	—
G. hirsuta	—	—	—	—	—	—	—	—	—	—
G. scitula	20	5	6	7	4	0.5	14	14	30	4.5
Orbulina universa	—	—	0.5	2	0.3	5	—	—	—	—
Sphaeroidina bulloides										
Benthonic Species %										
Cassidulina laevigata	—	—	55	54	24	—	—	—	49	—
C. subglobosa	—	—	—	9	—	—	—	—	—	—
Bolivina subaenariensis	—	—	—	—	—	—	—	—	7	—
B. sp. l	—	—	—	—	8	—	—	—	—	—
Bulimina aculeata	—	—	—	—	—	—	—	—	—	—
B. inflata	—	—	—	—	—	—	—	—	—	—
B. marginata	—	—	—	—	—	—	—	—	—	—
Uvigerina cf. peregrina	—	—	—	9	—	—	—	—	—	—
Quinqueloculina	—	—	—	—	8	—	100	—	42	—
Lagena	—	—	—	—	—	—	—	—	7	—
Triloculina tricarinata	—	—	—	—	—	—	—	—	—	—
Nonion	20	—	5	—	16	—	—	—	—	—
Cassidulina crassa	—	—	—	—	—	—	—	—	—	—
Pyrgo	—	—	—	—	—	—	—	—	—	—
Elphidium	—	100	5	9	—	—	—	—	—	—
Discorbis	80	—	15	—	—	—	—	—	—	—
Cibicides	—	—	—	—	8	50	—	—	—	—

Table 2. (*Cont.*)

Sample	Core 15						
	1501	1502	1504	1505	1506_1	1506_2	1507
Total No. of Specimens	190	4 470	122	46	2 432	1 818	2 622
Pelagic Species %							
Globigerina bulloides	47	36	53	36	44	78	38
G. inflata	19	21	—	12	8	—	—
G. pachyderma	—	13	1	8	22	6	38
G. dubia	—	0.7	—	—	0.3	—	—
Globigerinoides rubra	19	33	32	41	20	16	8
G. sacculifera	—	2	—	—	0.3	—	—
Globigerinella aequilateris	2	1	—	—	—	—	—
Globorotalia truncatulinoides	6	—	—	—	1	—	—
G. hirsuta	0.5	—	—	—	—	—	—
G. scitula	—	5	—	—	2	11	16
Orbulina universa	6	3	3	—	—	—	—
Sphaeroidina bulloides							
Benthonic Species %							
Cassidulina laevigata	20	—	20	40	9.8	9	60
C. subglobosa	20	—	20	—	7.0	45	6
Bolivina subaenariensis	—	—	—	—	33.6	9	—
B. sp. l	—	—	—	10	7.0	—	—
Bulimina aculeata	—	—	—	—	2.8	—	—
B. inflata	—	—	—	—	—	—	—
B. marginata	—	—	20	—	4.2	—	—
Uvigerina cf. peregrina	—	—	—	—	4.2	—	—
Quinqueloculina	—	—	20	—	7.0	9	6
Lagena	—	11	—	—	—	9	6
Triloculina tricarinata	—	—	20	—	—	—	—
Nonion	40	22	—	10	—	—	—
Cassidulina crassa	—	—	—	—	—	—	—
Pyrgo	—	—	—	—	—	—	—
Elphidium	—	—	—	—	—	—	6
Discorbis	—	—	—	—	4.2	—	—
Cibicides-	—	—	—	—	2.8	—	12

Table 2. (*Cont.*)

Sample	Core 16								
	1601	1603	1605	1607	1608	1609	1610	1612	1613
Total No. of Specimens	3 156	3 420	7 044	12 320	3 150	5 052	10 000	1 548	87
Pelagic Species %									
Globigerina bulloides	38	56	68	57	77	60	44	87	86
G. inflata	27	12	2	0.1	0.3	7	0.2	—	—
G. pachyderma	6	11	6	20	11	13	6	7	5
G. dubia	1.4	0.3	—	—	—	—	0.3	0.4	—
Globigerinoides rubra	15	4	11	2	6	13	10	3	—
G. sacculifera	4	9	2	0.1	0.3	1	0.2	0.4	1
Globigerinella aequilateris	0.6	—	—	—	—	—	—	—	—
Globorotalia truncatulinoides	1	0.3	—	—	—	—	—	—	—
G. hirsuta	0.2	—	—	—	—	—	—	—	—
G. scitula	3	7	11	20	4	6	40	2	7
Orbulina universa	3	—	—	—	—	—	—	0.2	—
Sphaeroidina bulloides	0.2								
Benthonic Species %									
Cassidulina laevigata	25	66	21	36	14	16	56	44	—
C. subglobosa	—	—	9	—	—	4	—	—	16
Bolivina subaenariensis	5	—	—	12	—	—	—	—	—
B. sp. 1	—	—	18	—	—	4	—	—	—
Bulimina aculeata	—	—	—	—	—	—	—	—	—
B. inflata	5	—	—	—	7	8	14	4	—
B. marginata	—	—	—	—	—	—	—	—	—
Uvigerina cf. peregrina	10	—	9	24	21	12	—	—	—
Quinqueloculina	15	33	6	12	7	4	28	16	16
Lagena	—	—	—	—	—	—	—	—	16
Triloculina tricarinata	—	—	—	—	—	4	—	—	—
Nonion	—	—	—	—	—	16	—	—	16
Cassidulina crassa	—	—	—	—	—	4	—	—	—
Pyrgo	5	—	3	—	7	—	—	8	16
Elphidium	—	—	9	—	7	—	—	—	—
Discorbis	—	—	6	—	—	4	—	—	—
Cibicides	35	—	18	—	21	20	—	12	16

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ENTRAINMENT OF AIR INTO A CUMULUS CLOUD

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ABSTRACT

A theory of convective clouds is presented, the fundamental hypothesis being that the ascending current in a cloud entrains air from its surroundings. A method is developed for computing the amount of entrainment from a knowledge of the temperature and specific humidity inside and outside the cloud. The concentration of water in the form of drops is also determined. Finally the theory is applied to some observations of trade cumulus made near San Juan, Puerto Rico.

1. Introduction

The picture of a cloud usually given [3, pp. 125–144] is that of a column or parcel of moist air ascending wet-adiabatically with no lateral mixing through an environment at rest. A more realistic picture is that given by Bjerknes [1]—the so-called 'slice method,' in which the environment is allowed to subside in order to preserve mass continuity.

The principle of the present theory is illustrated in fig. 1. As the cloud rises, air from the environment is drawn in and mixed with the cloud substance, thus modifying the mechanical and thermodynamic characteristics of the cloud. A steady state is assumed. Two important effects of the entrainment are the following:

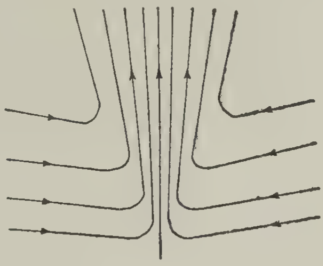

Fig. 1. Schematic vertical section of cloud column.

(a) The lapse rate within the cloud is not wet-adiabatic as previous theories predict.

(b) The vertical gradient of the concentration of liquid water within the cloud is different from that derived on the basis of other theories.

In some ways this notion of cumulus-cloud convection is similar to the jet-stream theories found so useful in aerodynamics by Tollmien [2, pp. 592–600] and others and in oceanography by Rossby [4]. The basic idea of the jet stream is that whenever a jet or current of fluid moves through a large body of fluid at rest there is entrainment of surrounding fluid into the moving portion, so that the mass flux increases with distance downstream. The theory of jets in simple liquids has not been extended to such relatively complicated conditions as those obtaining in the atmosphere over the range of altitudes and conditions in which cumulus clouds may appear.

The present study entails an important simplification which is not made in the usual jet-stream theories. It is assumed that there is horizontal homogeneity both inside and outside the cloud at each level, the change at the cloud boundary being discontinuous.

In the following paragraph the mass entrainment of outside air into the cloud column is computed as a function of the temperature and specific-humidity soundings inside and outside the cloud.

2. The mass flux gradient in a cloud

Let M be the upward mass flux across the entire cloud column at the level where the pressure is p. Let the flux of outside air into the cloud between the level p and a higher level $p - \delta p$ be δM. Since a steady state has been assumed, the flux at $p - \delta p$ is $M + \delta M$. The quantity M is a function of pressure. The quantity δp is an infinitesimal.

Let the actual soundings within the cloud be $T(p)$ and $q(p)$, the dry-bulb temperature and the specific humidity respectively—known as functions of pressure. Let the actual soundings in the clear, outside the cloud, be represented by the primed quantities $T'(p)$ and $q'(p)$. The fundamental problem is to discover the functional form of $M(p)$ that makes possible the observed values $T(p)$ and $q(p)$ on the supposition that outside air is drawn into the cloud.

The properties within the cloud at some particular level p are temperature T, specific humidity q, and concentration of liquid water W. At $p - \delta p$ the mass flux of the cloud is $M + \delta M$, the temperature is

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$T + \delta T$, the specific humidity is $q + \delta q$, and the liquid-water content is $W + \delta W$.

In rising from p to $p - \delta p$ the cloud undergoes a rather complex transformation which may be replaced by three simple steps. First, the temperature decreases because of the adiabatic decrease of pressure. Second, outside air is entrained and mixed with the cloud at the pressure $p - \delta p$. Third, a phase change achieves equilibrium between vapor and liquid phases.

It is necessary to frame the three steps into differential equations which express the transformation in properties.

In the first step the air rises, dry-adiabatically and with no condensation, from p to $p - \delta p$. The temperature changes from T to $T[(p - \delta p)/p]^{R/c_p}$ where R is the gas constant of moist air and c_p is the specific heat of air at constant pressure. It follows from the binomial theorem and from neglect of infinitesimals of order greater than one that

$$T\left[\frac{p - \delta p}{p}\right]^{R/c_p} = T\left[1 - \frac{R}{c_p}\frac{\delta p}{p}\right].$$

The second step is the process of entrainment and mixing. The flux δM actually entrained in the pressure interval from p to $p - \delta p$ is assumed to be entrained entirely at $p - \delta p$ and there mixed with the upward flux M. The temperature and specific humidity which result from this mixing at constant pressure are designated T^* and q^*. They are fictitious quantities. The point (q^*, T^*) is located somewhere along the straight line, called the *mixing line*, that passes through the two points

$$(q' + \delta q', T' + \delta T') \quad \text{and} \quad (q, T[1 - (R/c_p)(\delta p/p)]).$$

The position of (q^*, T^*) on the mixing line is related to the ratio $\delta M/M$. The mass of water vapor reaching $p - \delta p$ per unit time in the portion of the cloud rising from p to $p - \delta p$ must be Mq. The mass of water vapor introduced per unit time by the entrained air must be $(q' + \delta q')\delta M$. The sum of these must, by conservation, be equal to $(M + \delta M)q^*$, the amount in the final uncondensed mixture; hence, if second-order terms are dropped,

$$(M + \delta M)q^* = Mq + q' \,\delta M. \tag{1}$$

In an isobaric mixing process without phase change the heat is also conserved. The heat per unit time of the unmixed cloud air at $p - \delta p$ is $c_p MT[1 - (R/c_p)(\delta p/p)]$; that of the entrained portion is $c_p\,\delta M(T' + \delta T')$. The sum of these must equal the heat of the mixture, $c_p(M + \delta M)T^*$. The second-order terms may be dropped, so that

$$(M + \delta M)T^* = MT - MT(R/c_p)(\delta p/p) + \delta M\, T'. \tag{2}$$

The third step is the one in which condensation occurs in the mixture. Any condensation process at constant pressure in the q,T-plane must, to a first degree of approximation, occur along a straight line of slope $dT/dq = - L/c_p = - 2.47 \times 10^3$ C. This line must pass through the final, known point $(q + \delta q, T + \delta T)$ and is therefore determined. It intersects the mixing line. The equation of the condensation line may be written as

$$L(q + \delta q - q^*) = - c_p(T + \delta T - T^*). \tag{3}$$

The fictitious quantities T^* and q^* may be eliminated among equations (1, 2, 3). The second-order terms may be dropped, and the result is obtained that

$$M\,\delta q + q\,\delta M - q'\,\delta M = -\frac{c_p}{L}\left[M\,\delta T + T\,\delta M + MT\frac{R}{c_p}\frac{\delta p}{p} - T'\,\delta M\right]$$

Both sides may be divided by $M\,\delta p$ and the limit taken as δp approaches zero. A convenient final form is:

$$\frac{1}{M}\frac{dM}{dp} = \frac{\dfrac{dq}{dp} - \dfrac{c_p}{L}\dfrac{dT}{dp} - \dfrac{R}{L}\dfrac{T}{p}}{\dfrac{c_p}{L}(T - T') - (q - q')}. \tag{4}$$

Equation (4) enables the rate of mass entrainment into the cloud to be computed from any pair of soundings inside and outside the cloud.

3. The gradient of liquid water within the cloud

The flux of water substance at p is $M(q + W)$. The flux of water substance entrained is $(q' + \delta q')\delta M$. The sum of these two must equal the final flux of water substance in the mixed cloud at $p - \delta p$, that is, $(M + \delta M)(q + \delta q + W + \delta W)$. If second-order terms are dropped,

$$M(\delta q + \delta W) \doteq (q' - q - W)\delta M.$$

This may be divided by $M\,\delta p$; the limit as δp approaches zero is

$$\frac{dW}{dp} = (q' - q - W)\frac{1}{M}\frac{dM}{dp} - \frac{dq}{dp}. \tag{5}$$

Equations (4) and (5) give gradients of the quantities M and W. When the problem is to find M and W, a numerical integration must be used, starting from some known boundary condition; for example, one may choose the pressure at condensation level p_c as the place where $W(p_c) = 0$ and $M(p_c)$ is unit flux and proceed with a numerical integration from there upward. The graphical solution of this problem given in the following section illustrates the physical principles in a simple manner.

4. A graphical solution for dM/dp, given q, T, q', T'

The setting of all that follows is the q,T-plane. Points representing the soundings inside and outside the cloud may be plotted for each pressure level p_i:

$$p_i = p_0 - i\,\Delta p, \qquad i = 0, 1, 2, \cdots$$

where Δp is a finite pressure interval. Thus there are two sets of points, (q_i, T_i) and (q_i', T_i'). For convenience smooth curves may be drawn through these points (fig. 2). Now these steps may be followed:

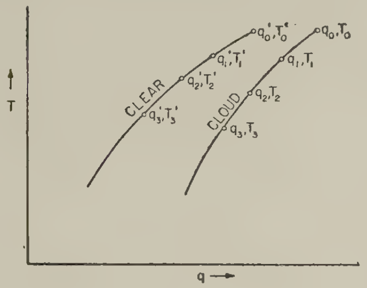

FIG. 2. Soundings in cloud and clear plotted on a q,T-plane.

1. The mass of the cloud at p_0 is M_0. Imagine it moved to p_1 without condensation. Since q remains constant, the process occurs along a vertical line. The point (q_0, T_1'') is determined by the dry-adiabatic lapse rate (fig. 3).

2. Now imagine that M_0 at this new T_1'' mixes with outside air drawn in at the level p_1, that is, at (q_1', T_1'). The temperature and humidity of the mixture must lie along the line $[(q_0, T_1'')(q_1', T_1')]$ at the point designated (q_1^*, T_1^*), as may be seen in fig. 4.

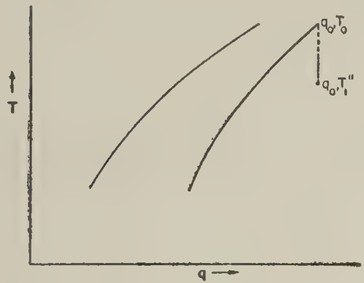

FIG. 3. Adiabatic rise of air from p_0 to p_1.

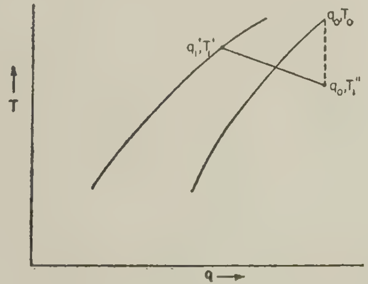

FIG. 4. Mixing of cloud with outside air without condensation.

3. When condensation occurs, the point representing the mixture moves along the line given by (3), the numerical value of dT/dq being everywhere approximately -2.47×10^3 C. But since this condensation process must end at the point (q_1, T_1) representing the actual cloud, the line through (q_1, T_1) and having the slope $dT/dq = -2.47 \times 10^3$ C determines (q_1^*, T_1^*), as seen in fig. 5.

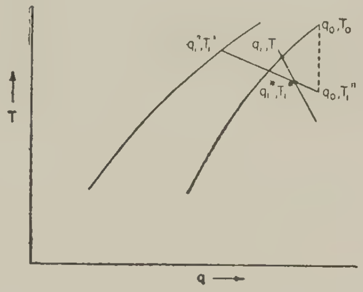

FIG. 5. Condensation of mixture to actual sounding.

4. The point of intersection is (q_1^*, T_1^*). The ratio of the lengths of the two segments equals the ratio of the flux into the cloud at this level to the upward flux at level p_0, that is,

$$\frac{M_1 - M_0}{M_0} = \frac{[(q_0, T_1'')(q_1^*, T_1^*)]}{[(q_1', T_1')(q_1^*, T_1^*)]}$$

The process may be continued. Perhaps the simplest technique is the following: Move (q_1^*, T_1^*) down vertically to (q_1^*, T_2''). Draw the line $[(q_1^*, T_2'')(q_1', T_2')]$. Finally, draw through (q_2, T_2) a line having the slope $dT/dq = -2.47 \times 10^3$ C, the point of intersection being (q_2^*, T_2^*), as seen in fig. 6.

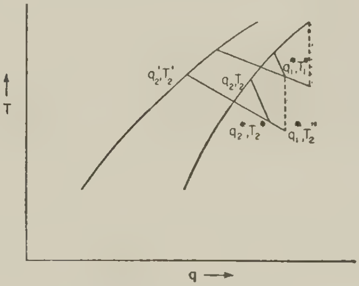

FIG. 6. Continuation of the graphical process for one more pressure interval.

The concentration of liquid in the cloud at any level p_i is simply $q_i^* - q_i$. The visible limit of the cloud is then at that level where $q_i^* = q_i$.

5. Application to soundings near San Juan

Airplane soundings inside and outside trade-wind cumulus were obtained in the course of an expedition

TABLE 1. Results in cloud soundings near San Juan, Puerto Rico, 1946 (19°20′ N, 65°20′ W approximately).

p (pressure in mb)	M (mass flux in arbitrary units)	W (liquid water concentration in g/kg)
	12 April	
941	1.00	0.00
931	1.30	0.05
921	1.69	0.05
911	2.29	0.03
901	3.12	0.02
891	3.33	0.01
	25 April	
940	1.00	0.00
930	1.24	0.20
920	1.46	0.39
910	1.72	0.30
900	2.11	0.25
890	2.80	0.10
	26 April	
936	1.00	0.00
926	1.07	0.30
916	1.18	0.40
906	1.27	0.60
896	1.39	0.50
886	1.50	0.50
876	1.61	0.60
866	1.72	0.70
856	1.85	0.80
846	2.01	0.80
836	2.17	0.80
826	2.29	0.90
816	2.56	0.90
806	2.75	0.70
	27 April	
948	1.00	0.00
938	1.18	0.15
928	1.36	0.20
918	1.36	0.40
908	1.36	0.60
898	1.36	0.90
888	1.36	1.15
878	1.40	1.25
868	1.46	1.25
858	1.58	1.20
848	1.66	1.25
838	1.90	1.00
828	2.30	0.60
818	2.50	0.50
808	2.70	0.50
	28 April	
940	1.00	0.00
930	1.00	0.20
920	1.01	0.40
910	1.07	0.50
900	1.20	0.35
890	1.44	0.30
880	1.53	0.45
870	1.60	0.45
860	1.76	0.20

from the Woods Hole Oceanographic Institution during April 1946 under the leadership of Dr. Jeffries Wyman and Mr. A. H. Woodcock. Wet- and dry-bulb temperatures were measured; consequently values of q and T and of q' and T' can be obtained. The resulting values of M and W found by the graphical method, the pressure increment being 10 mb, are shown in table 1. The value of M at the base of the cloud is arbitrarily chosen to be unit flux. The results indicate that the amount of entrained outside air is about twice the original volume. The concentration of liquid water passes through a maximum near the middle altitude of the cloud. Observations of the concentration of liquid water, had they been made, would have provided an excellent test of the hypothesis that surrounding air is entrained into the ascending column.

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Contribution No. 367

NOTE ON THE USE OF THE *T-S* CORRELATION FOR DYNAMIC HEIGHT ANOMALY COMPUTATIONS[1]

By

HENRY STOMMEL

Woods Hole Oceanographic Institution

1. The convenience of the bathythermograph for making rapid detailed surveys of the thermal structure in vertical sections of the ocean is leading to an accumulation of data on ocean temperatures far exceeding that on the corresponding salinities. Since dynamic height anomaly computations require a knowledge of both the temperature and the salinity as functions of depth, it is the purpose of this note to determine, in the case where only temperature data are available, whether or not it is possible to use the known *T-S* correlation for a given water mass to supply information on salinity which is sufficiently accurate to be used in dynamic height and current computations.

2. The functional relation between T and S, as shown by the *T-S* diagram for any particular water mass, is such that for a given temperature T the value of salinity S is given only within a certain "range of uncertainty," which is denoted by R_s. The quantity R_s varies for different water masses and also for different temperatures within the same water mass.

From a knowledge of the approximate dependence of R_s upon the pressure (depth) a rough estimate of the range of uncertainty R_D in the dynamic height may be made. For these purposes the *T-S* curve is divided into pressure intervals Δp of approximately constant R_s.

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Calculation of the mean range of uncertainty in the specific volume anomaly (indicated by R_δ) is then possible for each Δp. The products $R_\delta \cdot \Delta p$ are formed and summed up from the surface to the depth of the pressure reference level. The final quantity $\Sigma R_\delta \cdot \Delta p$ may be written as R_D. Because this represents the entire range of uncertainty in the determination of the dynamic height, the probable error in dynamic height may be taken as about $\pm \frac{1}{4} R_D$.

To facilitate this operation—which need merely be approximate—Table I has been constructed. It is prepared directly from the usual tables for δ_s (1, 4).

TABLE I—BRIEF TABLE FOR APPROXIMATE CALCULATION OF THE UNCERTAINTY IN SPECIFIC VOLUME ANOMALY FROM THE UNCERTAINTY IN SALINITY

Salinity Uncertainty R_s(°/oo)	*Specific Volume Anomaly Uncertainty* R_δ	*Salinity Uncertainty* R_s(°/oo)	*Specific Volume Anomaly Uncertainty* R_δ
0.00	0.00000	0.30	0.00023
.02	2	.40	30
.04	3	.50	38
.06	5	.60	46
.08	6	.70	53
.10	8	.80	61
.15	11	.90	69
.20	15	1.00	76
.25	19	2.00	152

As an example of the use of Table I, some stations made at the Grand Banks in June 1940 by the International Ice Patrol (3) are considered. Rather than include a great number of stations the discussion will be limited to the small area covered by stations 3275, 3276, 3277, and 3278. Upon plotting these data on a T-S plane it is immediately apparent that the curve may be broken up into five depth intervals

TABLE II—COMPUTATION SCHEME FOR DYNAMIC HEIGHT ANOMALY UNCERTAINTY FOR GRAND BANKS DATA

p (decibars)	Δp	R_s	R_δ	$R_\delta \cdot \Delta p$
0				
25	25	0.20	0.00015	0.00375
200	175	1.00	76	13300
300	100	0.20	15	1500
400	100	0.10	8	1000
1000	600	0.05	4	3000
				$R_D = 0.19175$

with an approximately constant R_s. The computation may then be made according to the scheme in Table II. From the results given in this table it is concluded that the probable error introduced into the dynamic height by trying to compute it with the use of the T-S correlation for the Grand Bank area would be excessive, about ± 0.05 meters.

An example showing the other extreme is found by determining, for purposes of illustration, the dynamic height of the 300 decibar surface above the 1000 decibar surface in the Sargasso Sea where the T-S correlation (2) is an extremely good one. The computation is given in Table III. The total range of uncertainty in dynamic height is of the order of 0.046 meters, and the probable error would then be ± 0.012 meters, which is good.

TABLE III—Computation Scheme for Dynamic Height Anomaly

p (decibars)	Δp	R_s	R_δ	$R_\delta \cdot \Delta p$
300				
400	100	0.12	0.00010	0.01000
1000	600	0.01	6	3600
				$R_D = 0.04600$

3. In those cases where the use of the T-S diagram for dynamic computations seems feasible (after a preliminary examination using the method in Section 2) a considerable simplification of the actual calculations is possible by constructing special tables for each water mass. These new tables would give the specific volume anomaly δ as a sum of only two terms, so that

$$\delta = [\tau] + [\tau, p].$$

An example of such tables appears in Section 5. The term $[\tau]$ includes the usual terms δ_s, δ_τ and $\delta_{s,\tau}$, whereas the term $[\tau, p]$ includes $\delta_{s,p}$ and $\delta_{\tau,p}$. It is also possible to include a column, in the table for $[\tau]$, which would give the probable error in δ due to the uncertainty involved in using the T-S curve. The accumulation of the errors may then be carried through by integration over depth, just as δ is integrated, and a more accurate estimate of the error will result than can be obtained through the use of Table I.

4. The range of uncertainty R_s in the salinity for a given temperature may arise from the following causes:

a. R_s will be very large wherever the slope of the T-S curve is small, as is the case in Baffin Bay water.

b. R_s will be large whenever seasonal variations and mixing occur. These conditions predominate, for example, near the surface.

c. Measurements of T and S at any station are made only for certain discrete values of the depth. Even if the precision of individual discrete measures were indefinitely high, an error would still be introduced due to the assumption that the specific volume varies linearly or "smoothly" between the points where the measures are made. Indeed, most recent experience with the bathythermograph indicates a wide prevalence of very irregular variations.

d. The accuracy of individual salinity measurements used in drawing up the T-S curve is limited, which fact implies an interesting point about the use of the T-S curve, since there may be an advantage in using the T-S curve for bodies like the Sargasso Sea instead of using individual measures. The value of R_s in the Sargasso Sea water below 300 meters is so small that it is possible that it arises from the inaccuracies of the salinity determinations themselves rather than from actual fluctuations in the composition of the water mass. In such a case the use of the T-S diagram would be more accurate than the use of individual measures for dynamic current computations.

5. In order to see how these ideas work out in practice, the following example has been prepared from "Atlantis" Stations 1637–1642 across the Gulf Stream at Onslow Bay. The T-S curve for this section shows that it is an intermediate case; it is not as scattered as in the case of the Grand Banks, but on the other hand, it is not as ideal as the one for the deep Sargasso Sea.

First, the anomaly of the dynamic height was computed by using the standard tables of Bjerknes and Sandstrom (1), from the formula

$$\delta = \delta_s + \delta_T + \delta_{s,T} + \delta_{s,P} + \delta_{T,P},$$

and by summing over the first 1000 meters of depth. The summations for stations 1637–8 were carried only for the entire depth to the ocean bottom, since in each of these instances the ocean depth is less than 1000 meters. This value of the dynamic height anomaly for each station is indicated in Table IV.

A T-S diagram for these six stations was then constructed, and a mean curve drawn. Both S and R_s were scaled off as functions of T; the results appear in Table V. Using this table and the Bjerknes-Sandstrom tables (1), special tables (as described above in Section 3) were constructed for this water mass, and these are included here as Tables VI and VII. Specific volume anomalies were then computed from Tables VI and VII and summed over the first 1000 meters. The resulting dynamic height anomalies appear in Table IV.

TABLE IV—COMPARISON OF DYNAMIC HEIGHT ANOMALIES OF "ATLANTIS" ONSLOW BAY STATIONS AS COMPUTED BY THE STANDARD TABLES OF BJERKNES AND SANDSTROM AND THOSE BY THE SPECIAL TABLES VI AND VII

(1) "Atlantis" Station Number	1639	1640	1641	1642	1637	1638
(2) Reference Level (meters)	1000	1000	1000	1000	189	461
(3) Dynamic height anomaly (meters) as computed by standard tables	1.690	1.756	1.711	1.472	0.473	1.027
(4) Dynamic height anomaly (meters) computed from Tables VI and VII	1.713	1.834	1.746	1.527	0.459	1.035
(5) Differences: (4) − (3) (meters)	0.023	0.078	0.035	0.055	−0.014	0.008

TABLE V—THE *T-S* RELATION FOR ONSLOW BAY, INCLUDING THE RANGE OF UNCERTAINTY OF SALINITY

Temperature T	*Salinity* S	*Uncertainty of Salinity* R_s
27.5	36.00	0.20
25.0	36.15	.20
22.5	36.35	.40
20.0	36.45	.30
17.5	36.40	.05
15.0	35.95	.05
12.5	35.62	.05
10.0	35.20	.04
7.5	35.08	.04
5.0	35.06	.04
2.5	35.04	.04

A comparison of the dynamic height anomalies, as computed by the standard technique and those computed by Tables VI and VII, shows (Table IV) that a considerable deviation exists between the results computed by the two different methods. This must be due to a variation of the water composition within the mass that was chosen. However, if the stations are divided into two groups—stations 1637–8, and stations 1639–42, the mean difference of the first group is negative, and that of the second group is + 0.047 meters. This suggests that there is a real change of water mass from one group to the other. As

TABLE VI—SPECIAL ONSLOW BAY TABLE OF THE CORRECTION [τ]

T	[τ]	T	[τ]
27	0.00438	14	0.00122
26	404	13	112
25	370	12	105
24	336	11	99
23	302	10	94
22	270	9	81
21	241	8	71
20	212	7	60
19	189	6	48
18	166	5	37
17	150	4	27
16	142	3	19
15	132	2	9

TABLE VII—SPECIAL ONSLOW BAY TABLE OF THE CORRECTION [τ, p]

$p \backslash T$	2½	5	7½	10	12½	15	17½	20	22½	25	27½
decibars	0	0	0	0	0	0	0	0	0	0	0
100	1	1	2	2	3	3	3	3	4	4	4
200	1	2	3	4	5	6	7	8	7	8	8
300	2	4	5	7	8	8	11	11	12	12	12
400	2	5	6	9	11	13	14	15	16	17	17
500	3	6	8	11	13	16	17	18	19	20	21
600	4	7	10	13	16	18	20	22	23	24	25
700	4	8	12	15	18	21	23	25	26	28	29
800	5	10	13	17	21	24	26	29	30	32	33
900	6	11	15	19	23	27	30	33	34	36	37
1000	6	12	17	21	26	30	33	36	38	39	41

a matter of fact, this may be seen from an examination of the *T-S* curve, where station 1637 differs most widely from the mean distribution. Had 1637 and 1638 been omitted from the construction of the *T-S* curve, the agreement of the two methods for the remaining stations would have been much better. The probable error of dynamic height anomaly in using the short tables instead of the standard tables for stations 1639–42 (omitting 1637–8 from the correlation diagram) would be about ± 0.02 meters. It is interesting to compare this probable error with that arising from the salinity measurements themselves. The error in the salinity measurements from these stations is estimated by Iselin (2) to be about $\pm\ 0.02\ ^{\circ}/_{\circ\circ}$ as a maximum. To this salinity error there corresponds a maximum error in dynamic height anomaly of about ± 0.02 meters.

As a result it appears that in certain restricted regions the *T-S* diagram may be used for rough dynamic computations. For more detailed survey work where great accuracy of the result is desired the method using the *T-S* diagram is clearly unsuitable.

6. It is certain that if more soundings were available for each of the stations there would have been more accurate values of dynamic height anomaly. However, there are only a certain number, and therefore there is little *a priori* reason to assume any particular kind of interpolation between these points. Some idea can be obtained of the inaccuracies introduced through a linear interpolation by omitting alternate soundings. For this purpose the data for each station were split into two sets of alternate soundings, and the dynamic height anomalies were computed for these as though they were the only data available in each case. The results, using the standard tables (1), are given in Table VIII, along with the differences between these values and the values computed from the complete data. In all cases it is seen that the dynamic height anomalies as computed by the two methods are considerably different—of the order of accuracy in which we are interested. It is essential to recognize, therefore, that the values in which all the data are used are subject to errors nearly of the same (though somewhat smaller) magnitude. This source of error—the interpolation error—appears in addition to the other errors. However, it is possible to eliminate the interpolation error almost completely from the dynamic height computations if use is made of a bathythermogram in conjunction with the more exact bottle data.

TABLE VIII. Error Due to Using a Linear Interpolation between Soundings as Indicated by Splitting the Soundings for Each Station into Two Alternate Sets

(1) "Atlantis" Station	1639	1640	1641	1642
(2) Dynamic height anomaly from complete data (meters)	1.690	1.756	1.711	1.472
(3) Dynamic height anomaly from first half of soundings taken alternately	1.711	1.803	1.754	1.453
(4) Dynamic height anomaly from second half of soundings taken alternately	1.707	1.765	1.698	1.429
(5) Difference: (3) − (2)	0.021	0.047	0.043	−0.019
(6) Difference: (4) − (2)	0.017	0.009	−0.013	−0.043

It would be unwise to claim too much for the techniques proposed in this note. However, it may be possible (for certain very homogeneous water masses such as the Sargasso Sea), by judicious use of the *T-S* correlation curve, the bathythermogram, the usual bottle samples and temperatures, that errors due to both individual measurements of salinity and interpolation may be largely suppressed, with the result that the dynamic heights so obtained would be certain to an additional half decimal place or better.

ACKNOWLEDGMENT

There is very little which is original with the writer in the present note, since it is the result of the thoughts of a number of people. The possibility of using the *T-S* diagram for dynamic computations was first mentioned to the writer by Dr. C.-G. Rossby. From subsequent correspondence it appears that Mr. C. O'D. Iselin and Mr. Floyd Soule had considered the idea years ago. An estimate of the desired accuracy in work of this kind was obtained from some unpublished notes of Dr. R. B. Montgomery. In addition, the writer has had the opportunity to discuss these and related matters with Messrs. Frederick Fuglister, V. P. Starr and A. C. Vine.

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From a knowledge of the approximate dependence of R_s upon the pressure (depth) a rough estimate of the range of uncertainty R_D in the dynamic height may be made. For these purposes the *T-S* curve is divided into pressure intervals Δp of approximately constant R_s.

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An example showing the other extreme is found by determining, for purposes of illustration, the dynamic height of the 300 decibar surface above the 1000 decibar surface in the Sargasso Sea where the *T-S* correlation (2) is an extremely good one. The computation is given in Table III. The total range of uncertainty in dynamic height is of the order of 0.046 meters, and the probable error would then be ± 0.012 meters, which is good.

TABLE III—COMPUTATION SCHEME FOR DYNAMIC HEIGHT ANOMALY

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1000	600	0.01	6	3600
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3. In those cases where the use of the *T-S* diagram for dynamic computations seems feasible (after a preliminary examination using the method in Section 2) a considerable simplification of the actual calculations is possible by constructing special tables for each water mass. These new tables would give the specific volume anomaly δ as a sum of only two terms, so that

$$\delta = [\tau] + [\tau, p] .$$

An example of such tables appears in Section 5. The term $[\tau]$ includes the usual terms δ_s, δ_τ and $\delta_{s,\tau}$, whereas the term $[\tau, p]$ includes $\delta_{s,P}$ and $\delta_{\tau,P}$. It is also possible to include a column, in the table for $[\tau]$, which would give the probable error in δ due to the uncertainty involved in using the *T-S* curve. The accumulation of the errors may then be carried through by integration over depth, just as δ is integrated, and a more accurate estimate of the error will result than can be obtained through the use of Table I.

4. The range of uncertainty R_s in the salinity for a given temperature may arise from the following causes:

a. R_s will be very large wherever the slope of the *T-S* curve is small, as is the case in Baffin Bay water.

b. R_s will be large whenever seasonal variations and mixing occur. These conditions predominate, for example, near the surface.

c. Measurements of T and S at any station are made only for certain discrete values of the depth. Even if the precision of individual discrete measures were indefinitely high, an error would still be introduced due to the assumption that the specific volume varies linearly or "smoothly" between the points where the measures are made. Indeed, most recent experience with the bathythermograph indicates a wide prevalence of very irregular variations.

d. The accuracy of individual salinity measurements used in drawing up the T-S curve is limited, which fact implies an interesting point about the use of the T-S curve, since there may be an advantage in using the T-S curve for bodies like the Sargasso Sea instead of using individual measures. The value of R_s in the Sargasso Sea water below 300 meters is so small that it is possible that it arises from the inaccuracies of the salinity determinations themselves rather than from actual fluctuations in the composition of the water mass. In such a case the use of the T-S diagram would be more accurate than the use of individual measures for dynamic current computations.

5. In order to see how these ideas work out in practice, the following example has been prepared from "Atlantis" Stations 1637–1642 across the Gulf Stream at Onslow Bay. The T-S curve for this section shows that it is an intermediate case; it is not as scattered as in the case of the Grand Banks, but on the other hand, it is not as ideal as the one for the deep Sargasso Sea.

First, the anomaly of the dynamic height was computed by using the standard tables of Bjerknes and Sandstrom (1), from the formula

$$\delta = \delta_s + \delta_T + \delta_{s,\,T} + \delta_{s,\,P} + \delta_{T,\,P}\,,$$

and by summing over the first 1000 meters of depth. The summations for stations 1637–8 were carried only for the entire depth to the ocean bottom, since in each of these instances the ocean depth is less than 1000 meters. This value of the dynamic height anomaly for each station is indicated in Table IV.

A T-S diagram for these six stations was then constructed, and a mean curve drawn. Both S and R_s were scaled off as functions of T; the results appear in Table V. Using this table and the Bjerknes-Sandstrom tables (1), special tables (as described above in Section 3) were constructed for this water mass, and these are included here as Tables VI and VII. Specific volume anomalies were then computed from Tables VI and VII and summed over the first 1000 meters. The resulting dynamic height anomalies appear in Table IV.

TABLE IV—COMPARISON OF DYNAMIC HEIGHT ANOMALIES OF "ATLANTIS" ONSLOW BAY STATIONS AS COMPUTED BY THE STANDARD TABLES OF BJERKNES AND SANDSTROM AND THOSE BY THE SPECIAL TABLES VI AND VII

(1) "Atlantis" Station Number	1639	1640	1641	1642	1637	1638
(2) Reference Level (meters)	1000	1000	1000	1000	189	461
(3) Dynamic height anomaly (meters) as computed by standard tables	1.690	1.756	1.711	1.472	0.473	1.027
(4) Dynamic height anomaly (meters) computed from Tables VI and VII	1.713	1.834	1.746	1.527	0.459	1.035
(5) Differences: (4) − (3) (meters)	0.023	0.078	0.035	0.055	−0.014	0.008

TABLE V—THE *T-S* RELATION FOR ONSLOW BAY, INCLUDING THE RANGE OF UNCERTAINTY OF SALINITY

Temperature T	*Salinity* S	*Uncertainty of Salinity* R_s
27.5	36.00	0.20
25.0	36.15	.20
22.5	36.35	.40
20.0	36.45	.30
17.5	36.40	.05
15.0	35.95	.05
12.5	35.62	.05
10.0	35.20	.04
7.5	35.08	.04
5.0	35.06	.04
2.5	35.04	.04

A comparison of the dynamic height anomalies, as computed by the standard technique and those computed by Tables VI and VII, shows (Table IV) that a considerable deviation exists between the results computed by the two different methods. This must be due to a variation of the water composition within the mass that was chosen. However, if the stations are divided into two groups—stations 1637–8, and stations 1639–42, the mean difference of the first group is negative, and that of the second group is + 0.047 meters. This suggests that there is a real change of water mass from one group to the other. As

TABLE VI—SPECIAL ONSLOW BAY TABLE OF THE CORRECTION [τ]

T	[τ]	T	[τ]
27	0.00438	14	0.00122
26	404	13	112
25	370	12	105
24	336	11	99
23	302	10	94
22	270	9	81
21	241	8	71
20	212	7	60
19	189	6	48
18	166	5	37
17	150	4	27
16	142	3	19
15	132	2	9

TABLE VII—SPECIAL ONSLOW BAY TABLE OF THE CORRECTION [τ, p]

p \ T	2½	5	7½	10	12½	15	17½	20	22½	25	27½
decibars	0	0	0	0	0	0	0	0	0	0	0
100	1	1	2	2	3	3	3	3	4	4	4
200	1	2	3	4	5	6	7	8	7	8	8
300	2	4	5	7	8	8	11	11	12	12	12
400	2	5	6	9	11	13	14	15	16	17	17
500	3	6	8	11	13	16	17	18	19	20	21
600	4	7	10	13	16	18	20	22	23	24	25
700	4	8	12	15	18	21	23	25	26	28	29
800	5	10	13	17	21	24	26	29	30	32	33
900	6	11	15	19	23	27	30	33	34	36	37
1000	6	12	17	21	26	30	33	36	38	39	41

a matter of fact, this may be seen from an examination of the *T-S* curve, where station 1637 differs most widely from the mean distribution. Had 1637 and 1638 been omitted from the construction of the *T-S* curve, the agreement of the two methods for the remaining stations would have been much better. The probable error of dynamic height anomaly in using the short tables instead of the standard tables for stations 1639–42 (omitting 1637–8 from the correlation diagram) would be about ± 0.02 meters. It is interesting to compare this probable error with that arising from the salinity measurements themselves. The error in the salinity measurements from these stations is estimated by Iselin (2) to be about ± 0.02 °/₀₀ as a maximum. To this salinity error there corresponds a maximum error in dynamic height anomaly of about ± 0.02 meters.

As a result it appears that in certain restricted regions the *T-S* diagram may be used for rough dynamic computations. For more detailed survey work where great accuracy of the result is desired the method using the *T-S* diagram is clearly unsuitable.

6. It is certain that if more soundings were available for each of the stations there would have been more accurate values of dynamic height anomaly. However, there are only a certain number, and therefore there is little *a priori* reason to assume any particular kind of interpolation between these points. Some idea can be obtained of the inaccuracies introduced through a linear interpolation by omitting alternate soundings. For this purpose the data for each station were split into two sets of alternate soundings, and the dynamic height anomalies were computed for these as though they were the only data available in each case. The results, using the standard tables (1), are given in Table VIII, along with the differences between these values and the values computed from the complete data. In all cases it is seen that the dynamic height anomalies as computed by the two methods are considerably different—of the order of accuracy in which we are interested. It is essential to recognize, therefore, that the values in which all the data are used are subject to errors nearly of the same (though somewhat smaller) magnitude. This source of error—the interpolation error—appears in addition to the other errors. However, it is possible to eliminate the interpolation error almost completely from the dynamic height computations if use is made of a bathythermogram in conjunction with the more exact bottle data.

TABLE VIII. Error Due to Using a Linear Interpolation between Soundings as Indicated by Splitting the Soundings for Each Station into Two Alternate Sets

(1) "Atlantis" Station	1639	1640	1641	1642
(2) Dynamic height anomaly from complete data (meters)	1.690	1.756	1.711	1.472
(3) Dynamic height anomaly from first half of soundings taken alternately	1.711	1.803	1.754	1.453
(4) Dynamic height anomaly from second half of soundings taken alternately	1.707	1.765	1.698	1.429
(5) Difference: (3) − (2)	0.021	0.047	0.043	−0.019
(6) Difference: (4) − (2)	0.017	0.009	−0.013	−0.043

It would be unwise to claim too much for the techniques proposed in this note. However, it may be possible (for certain very homogeneous water masses such as the Sargasso Sea), by judicious use of the *T-S* correlation curve, the bathythermogram, the usual bottle samples and temperatures, that errors due to both individual measurements of salinity and interpolation may be largely suppressed, with the result that the dynamic heights so obtained would be certain to an additional half decimal place or better.

ACKNOWLEDGMENT

There is very little which is original with the writer in the present note, since it is the result of the thoughts of a number of people. The possibility of using the *T-S* diagram for dynamic computations was first mentioned to the writer by Dr. C.-G. Rossby. From subsequent correspondence it appears that Mr. C. O'D. Iselin and Mr. Floyd Soule had considered the idea years ago. An estimate of the desired accuracy in work of this kind was obtained from some unpublished notes of Dr. R. B. Montgomery. In addition, the writer has had the opportunity to discuss these and related matters with Messrs. Frederick Fuglister, V. P. Starr and A. C. Vine.

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Contribution No. 368

A THEORETICAL ANALYSIS OF THE ZOOPLANKTON POPULATION OF GEORGES BANK[1]

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Studies by Fleming (1939), Riley and Bumpus (1946), and Riley (1946) of the seasonal variations of marine phytoplankton populations have resulted in the development of a growth budget in which the rate of change of the population is balanced against the rates of all the processes that increase or decrease the organic content of the population. The fundamental basis of this type of analysis is a differential equation in which the rate of change of the carbon content of the phytoplankton at any time is equal to the difference between the rate of accumulation of carbon by photosynthesis and the rates of dissipation by respiration, grazing, and natural death. Furthermore, since interest is centered in the seasonal cycle rather than long period fluctuations, it is assumed for practical purposes that over a period of one year the sum of the variations expressed by the equation is equal to zero. In the first two papers cited above, a study was made of the period of the spring diatom flowering in the Georges Bank area of the Gulf of Maine and in the English Channel where the budgets proved useful in describing quantitatively the phytoplankton-zooplankton grazing relationship. In the third paper, a more elaborate but somewhat empirical treatment of the same general type was used to evaluate the entire yearly phytoplankton cycle on Georges Bank.

The advantage of this method is that the balancing of the budget permits an estimate of the overall accuracy of the results. It is therefore a useful tool in putting ecological theories to a quantitative test. The disadvantage is that it requires detailed quantitative information about many processes, some of which are only poorly understood. Therefore, until more adequate knowledge is obtained, any application of the method must contain some arbitrary assumptions and many errors due to over-simplification.

This type of treatment is not necessarily limited to phytoplankton studies. Any population that is ecologically homogeneous may be

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considered in an analogous way. For example, the animals which live by grazing on phytoplankton may be analyzed by an equation such as:

$$\frac{dH}{dt} = H(A\text{-}R\text{-}C\text{-}D)\,, \tag{1}$$

in which:

H = the herbivore population;
A = the rate of assimilation of food by the herbivores;
R = their respiration rate;
C = the rate of consumption of herbivores by their predators;
D = the herbivore death rate.

Then the size of the population at the end of time t is determined by the equation:

$$H_t = H_0 e^{(A-R-C-D)t}. \tag{2}$$

While the theory is simple enough, the practical application is full of uncertainty because we know so little about the physiology of herbivores and about their predators. The writer feels that it is worthwhile to include such an analysis in the general study of Georges Bank plankton, but the available information is only a small fraction of what is needed for the work, and the results are therefore to a large degree speculative.

The data in the present analysis are derived largely from the two papers referred to previously. The zooplankton population on Georges Bank, shown in Fig. 27, was estimated as grams of carbon per m^2 of sea surface, determined by applying a conversion factor to the measurements of zooplankton volume. Herbivores constitute the main bulk of the zooplankton. Since there is no simple and accurate method of quantitatively allowing for that part of the zooplankton which is carnivorous, it will be assumed that the population of herbivores is equal to the total zooplankton.

Assimilation. The assimilation rate is strictly defined as grams of carbon taken into the herbivore tissues (and therefore available for growth or energy) per day per gram of carbon in the herbivore population. Since the assimilation rate does not readily lend itself to quantitative measurement, it is necessary to use indirect evidence to derive a practical definition which is at best an approximation. This definition is as follows:

The assimilation rate is 0.0075 P, where P represents grams of phytoplankton carbon per m^2, except when this value exceeds 8 per cent of the animals' weight per day, which is set as the maximum limit of the assimilation rate.

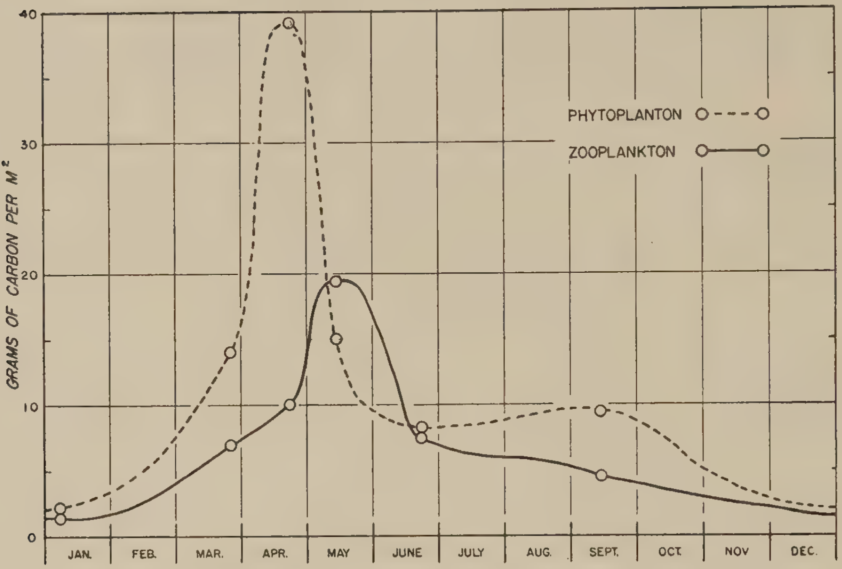

Figure 27. Seasonal cycles of phytoplankton and zooplankton on Georges Bank.

The definition is based on the following line of reasoning: It is generally believed that a unit quantity of zooplankton filters the food from a constant volume of water per unit time and therefore eats a constant fraction of the phytoplankton population per day irrespective of the absolute size of the population. This presupposes that the feeding rate is not affected by seasonal changes in temperature, which may not be strictly true, although previous discussion of the subject (Riley, 1946) indicated that on Georges Bank the feeding rate was probably independent of temperature. In the paper just referred to, it was estimated that the fraction of the phytoplankton consumed by a unit quantity of zooplankton (1 g. carbon per m^2) was 0.0075. Therefore, the daily rate of consumption of food by herbivores is 0.0075 P, where P represents grams of phytoplankton carbon. The phytoplankton population is shown in Fig. 27, and the consumption rate derived from it is the upper curve in Fig. 28A.

In a study of the plankton of the English Channel, Harvey, Cooper, Lebour and Russell (1935) concluded that utilization (the ratio of assimilation to consumption) was very near unity through most of the year, but that the spring diatom flowering provided the animals with more food than they could use, so that some was excreted in a semidigested condition. The same thing appears to occur in the

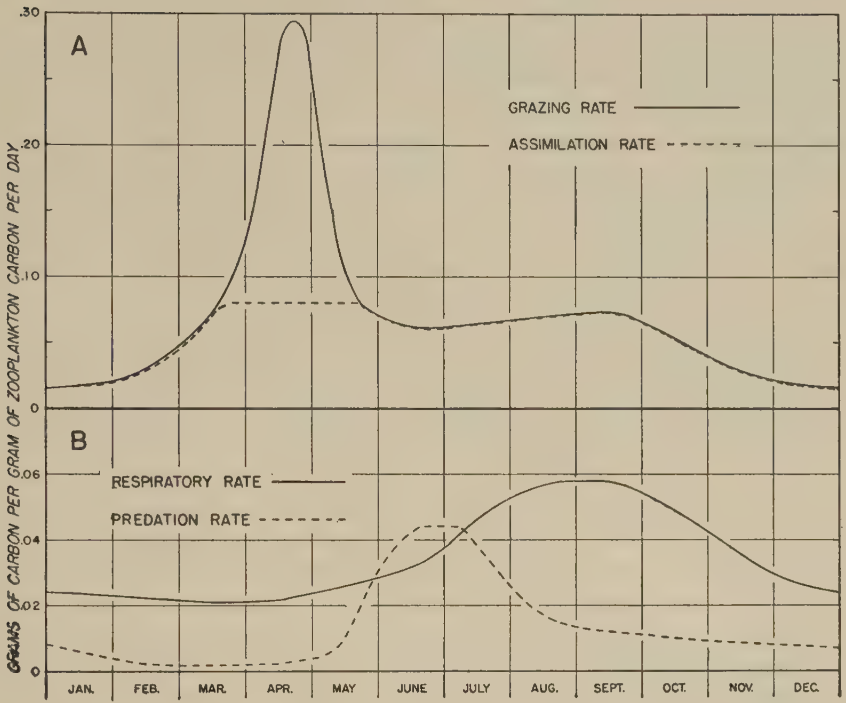

Figure 28. Processes of accumulation and loss of organic matter by Georges Bank zooplankton. A. Estimated rates of consumption and assimilation of phytoplankton food. B, Estimated rates of respiration and consumption of zooplankton by its predators.

Georges Bank area, for although the growth budget for phytoplankton indicates that consumption continues at a constant rate through the spring flowering, the amount consumed is at least twice as much as is needed to account for the observed rate of animal growth. Furthermore, the zooplankton appears to have attained its maximum rate of spring growth in late March before the phytoplankton reached its peak and to have maintained this rate until about the middle of May, when the diatom flowering was largely finished. It seems likely, therefore, that the assimilation rate during the whole of the spring flowering was no larger than the consumption rate of 0.080 observed at the beginning and end of this period. The definition therefore sets 0.080 (8 per cent per day) as the maximum rate of assimilation, and during the remainder of the year it is assumed that assimilation approximately equals consumption. The final result is shown by the broken curve in Fig. 28A.

Respiration. It will be assumed that the respiratory rate increases with an increase in temperature and is not affected by any other factor. Thus

$$R = rf(T)\,, \tag{3}$$

in which:

R = the respiratory rate in g. carbon consumed per g. of herbivore carbon per day;
r = the respiratory rate at 0° C = 0.019 (1.9% of the animals' weight per day);
T = Temperature (°C), the seasonal cycle of which is shown in Fig. 29;
$f(T)$ = the ratio of the respiratory rate at any temperature T to the rate at 0°, as shown in Fig. 29, inset.

This definition is derived from a study of the respiration of the copepod *Calanus finmarchicus* by Marshall, Nicholls and Orr (1935). They found that the increase in the respiratory rate with temperature

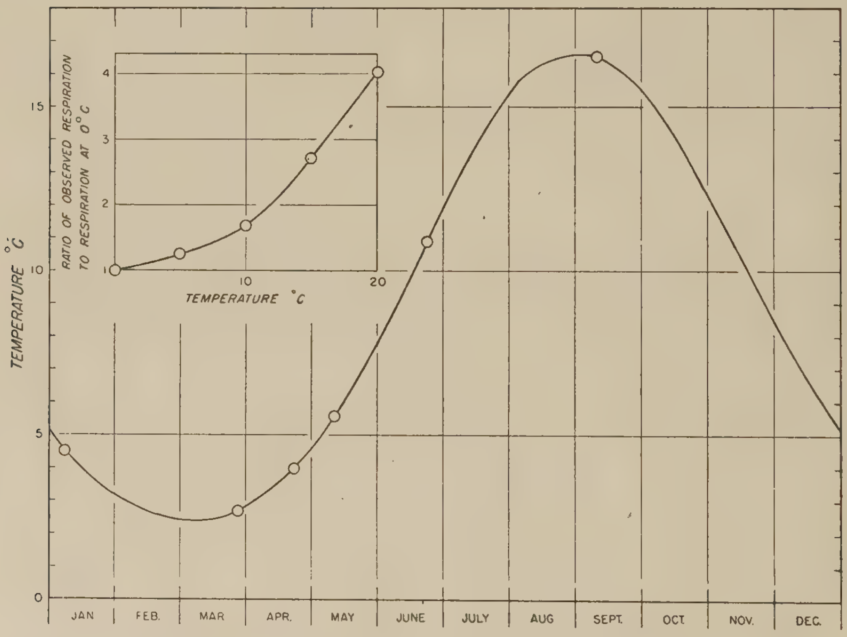

Figure 29. Seasonal temperature change on Georges Bank. Inset, estimated effect of temperature on zooplankton respiration.

did not have an easily defined form such as the van't Hoff law; hence in the present treatment it is necessary to use a graphical definition of the type shown in the inset in Fig. 29. Each point on the curve is obtained by averaging their experiments with stage *V* copepodites and adult males and females. Using this average curve as a basis, a value for the constant r can now be derived from each of the experiments, regardless of the temperature at which it was conducted. The experiments yield a large range of values, from 0.006 to 0.029, which average 0.019. This average value for the constant is used in the present report. The seasonal change in the estimated respiratory rate is shown in Fig. 28B.

Predation and loss by other causes. It will be assumed that herbivore predators expend a constant feeding effort irrespective of the amount of food available. Then the total amount of food eaten will be proportional to the product of predators and prey, and the rate of consumption of the prey will be proportional to the number of predators. This is similar to the assumption previously made about the phytoplankton-zooplankton grazing relationship, and it leads to an equation such that:

$$C = cS \tag{4}$$

where:

C = the rate of consumption of herbivores;
c = a constant;
S = the quantity of herbivore predators.

It seems likely that sagittae are the most important herbivore predators in the Georges Bank area, since they are numerically very abundant and since, according to LeBour (1922, 1923), they commonly feed on copepods, although fish larvae and other sagittae also constitute part of their diet. Other predators, such as mackerel, the pelagic young of various other fishes, decapod larvae and jellyfish are much less numerous than the sagittae; moreover, the quantitative aspects of their part in the food chain are very uncertain, and therefore, they are not included in the analysis of predation.

Fig. 30 is the seasonal cycle of *Sagitta elegans*, the only quantitatively important species of sagittae on Georges Bank, based on data published by Clarke, Pierce and Bumpus (1943). The curve shows a minimum point in early spring and a maximum in early or midsummer. The maximum is poorly defined due to the lack of summer data. However, it is clear that the time when the sagittae increased most rapidly coincided with the seasonal peak in total zooplankton, just as the latter increased most rapidly at the time of the diatom flowering. Thus there was a lag period of roughly a month in successive constituents of the food chain.

Little is known about the feeding rate of sagittae, or about the quantity of organic material involved. It is not possible, therefore,

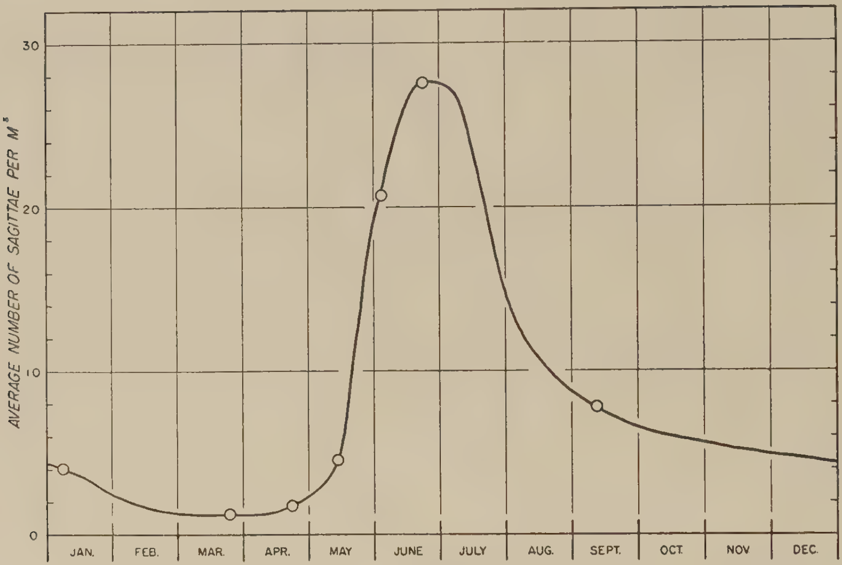

Figure 30. Seasonal change in the concentration of *Sagitta elegans* on Georges Bank.

to assign an experimentally determined value for the constant c in equation (4). An approximation can be obtained by statistical methods as will be shown later. However, it is first necessary to consider the herbivore death rate.

It will be assumed that the death rate D is constant. In this category are lumped several processes, such as natural death, predation by animals other than sagittae, and dilution of the population by water movements. None of these factors is actually constant, with the possible exception of natural death, although there is a slight factual basis in that the net loss is more uniform than any one of its component factors, for predation is certain to be more important during the summer season and loss by water transport more important during the winter.

On the basis of these assumptions, equation (1) is rearranged so that the terms that have already been evaluated are on the left, with predation and death on the right:

$$A - R - \frac{1}{H}\left(\frac{dH}{dt}\right) = cS + D.$$

Numerical values for the left-hand side of the equation are determined for various times of the year, and corresponding values for S are read

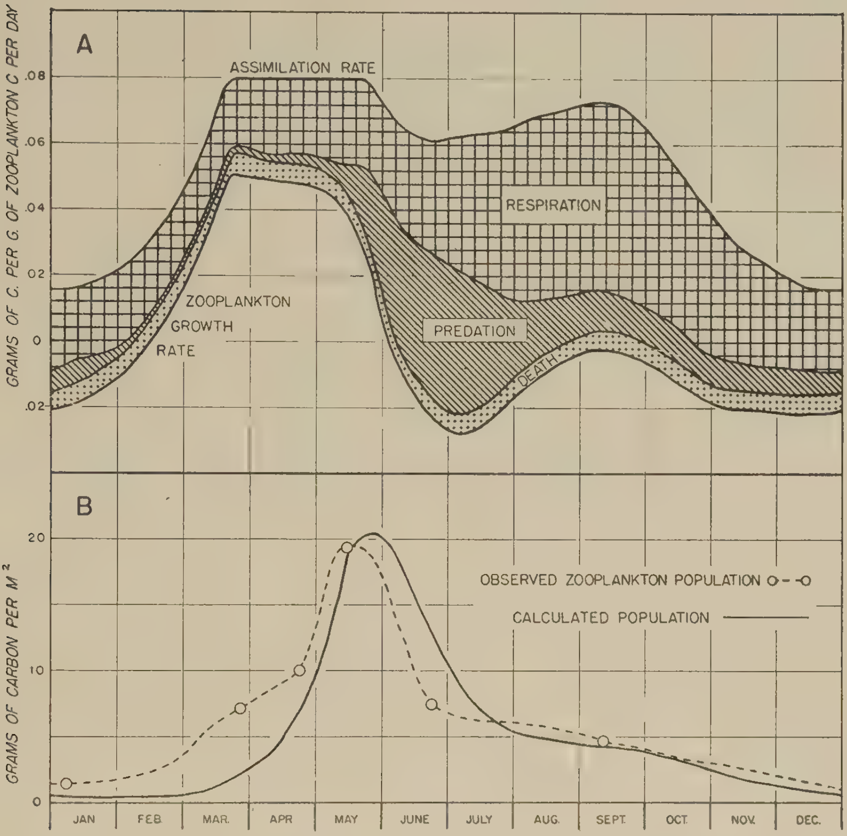

Figure 31. A. Summation of zooplankton growth processes. For complete explanation, see text (p. 111). B. Observed zooplankton seasonal cycle and the theoretical population curve calculated on the basis of seasonal variations in environmental factors.

from the curve in Fig. 30. The constants c and D can then be estimated statistically by the least squares method, and it is found that

$$A - R + \frac{1}{H}\left(\frac{dH}{dt}\right) = 0.0016\,S + 0.006\,,$$

where S is the number of sagittae per m^3.

Seasonal change in the herbivore population. Fig. 31A is a graphical summation of the various factors that are believed to affect the seasonal rate of change of the herbivore population. The upper curve is the estimated rate of assimilation A. When the respiration rate R is subtracted from the assimilation rate, the result is the second curve. From it are subtracted successively the rate of consumption C and the death rate by other causes D, yielding the bottom curve which is the estimated rate of change of the population. This curve can be approximately integrated by assigning a mean value for the rate of change during successive short intervals of time and by applying these mean rates to equation (2). The absolute size of the population, of course, depends on the integration constant H_o, and this constant is arbitrarily chosen so that the average population will approximate the observed one. The results are shown in Fig. 31B, in which the solid line is the theoretical population curve, and the observed population is indicated by dots connected with a broken line. The curves differ in that the ratio of maximum to minimum population is greater in the theoretical curve, and growth in the late winter and early spring is much slower than that of the observed population. Otherwise fair agreement is obtained, and it appears likely that the general mode of attack is correct, although each step in the analysis would be much improved by further study.

SUMMARY

1. A theoretical analysis of the seasonal cycle of zooplankton in the Georges Bank area is presented. An equation is set up in which the rate of change of the herbivore population in respect to time is equal to the difference between the rate of assimilation of organic material by feeding on the phytoplankton and the rate of dissipation by respiration, predation, and loss by various other causes.

2. With the aid of experimental data and statistical procedures, numerical values are assigned to the constants in the equation. It is then possible to construct a theoretical curve for the herbivore seasonal cycle which is in general agreement with the observed population.

3. This type of analysis is particularly useful in plankton work, since it utilizes all the available quantitative information on the biology of a particular group of organisms in a way that permits testing the overall accuracy of the results.

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Contribution No. 369

SEASONAL FLUCTUATIONS OF THE PHYTOPLANKTON POPULATION IN NEW ENGLAND COASTAL WATERS[1]

By

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An analysis of the seasonal phytoplankton cycle of the Georges Bank area of the Gulf of Maine (Riley, 1946) has shown that fluctuations in the population are largely controlled by the seasonal variations of a few environmental factors. An equation was developed in which the rate of change of the population in respect to time was equal to the photosynthetic rate minus the respiratory rate minus the rate of removal of the population by grazing. These rates were in turn evaluated in terms of incident solar radiation, transparency of the water, the depth of the mixed surface layer, the quantity of phosphate, temperature, and the amount of zooplankton.

This type of analysis, introduced by Fleming (1939) and elaborated in the paper referred to above, can be made to serve a variety of purposes in marine biology. It can be applied to zooplankton populations (Riley, 1947) or other ecologically homogeneous groups of organisms. It may also be used to study regional variations in plankton cycles. An approach to this problem is made in the present paper.

Bigelow (1926), Bigelow, Lillick and Sears (1940), and others have noted the considerable differences in seasonal phytoplankton cycles that occur in the waters off the New England coast. The spring flowering is likely to begin any time between January and early March in the shallow coastal waters, in late March or early April on the offshore banks, and in April or May in the continental slope waters and the deep basins of the Gulf of Maine. The spring diatom burst tends to be smaller in coastal areas than in deep water and may be overshadowed by sporadic flowerings in the late summer and autumn. Autumn flowerings are small or nonexistent in the deeper water. And finally, the total variation between maximum and minimum populations is greater in deep water.

The causes of these differences are not immediately apparent. The basic environment is much the same throughout the area, although

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there are small differences that are largely related to the depth of water—differences in transparency, thermal structure, and in the amount and presumably in the availability of nutrient salts. Perhaps these differences are enough to account for the observed variations in phytoplankton cycles, or perhaps species differences or some environmental factors, which are as yet unmeasured, must be considered.

The type of analysis that was made of the Georges Bank plankton provides a mode of attack on this problem. If plankton growth in the various parts of the region is largely dependent on a few commonly measured environmental factors, then an equation that predicts growth in terms of these factors should be equally applicable in any area. If it is not applicable, either the equation is not properly constructed or there is a certain amount of species variability that cannot be analyzed mathematically.

PHYTOPLANKTON OF THE WOODS HOLE AREA

Lillick (1937) published an account of phytoplankton collections made near the western entrance of Vineyard Sound (Lat. 41° 17′ 35″ N., Long. 71° 00′ 00″ W.) during the period from July 1935 to August 1936. The total cell counts shown in Fig. 32 demonstrate a seasonal cycle which is in general typical of New England coastal waters. The phytoplankton studies were accompanied by determinations of temperature, salinity, phosphate, and nitrate, and in addition zooplankton collections were made (Clarke and Zinn, 1937), and the transparency of the water was measured during the period from November 1935 to September 1936 (Clarke, 1938). Altogether it is the most complete survey that has been made in these waters and is in most respects suitable for comparison with the Georges Bank seasonal cycle.

On Georges Bank it was found (Riley, 1946) that the seasonal change in the size of the total population could be determined with a fair degree of accuracy by the equation

$$\frac{dP}{dt} = P\left[\frac{pI_\circ}{kz_1}(1 - e^{-kz_1})\,(1 - N)\,(1 - V) - R_\circ e^{rT} - gZ\right], \qquad (1)$$

in which:

P = phytoplankton population measured as grams of carbon per m^2;
p = a photosynthetic constant = g. of carbon produced per g. of phytoplankton carbon per day per average rate of solar radiation;
$I_\circ$ = average daily rate of incident solar radiation in g. cal. per cm^2 per minute;
k = extinction coefficient for light transmission;

z_1 = maximum depth of the euphotic zone, defined as the depth at which the light intensity is 0.0015 g. cal. per cm^2 per minute;

$(1 - N)$ = reduction in photosynetic rate caused by nutrient depletion, defined as phosphate concentration at the surface in mg.-at. of P per m^3 divided by 0.55 when the concentration is less than 0.55;

$(1 - V)$ = reduction in photosynthetic rate caused by dilution of the population by vertical turbulence, defined as the ratio of z_1 to the depth of the mixed layer when the latter is greater than z_1;

R_o = phytoplankton respiratory rate at 0° C;

r = rate of change of the respiratory rate with temperature, the value of r being set so that the rate is doubled by a ten degree increase in temperature;

T = temperature in degrees Centigrade;

g = rate of reduction of phytoplankton by the grazing of a unit quantity of zooplankton (one gram of zooplankton carbon);

Z = total quantity of zooplankton in grams of carbon per m^2.

Numerical values for the constants, obtained from various experimental observations, were as follows: $p = 2.5$, $R_o = 0.0175$, $r = 0.069$, and $g = 0.0075$.

Seasonal variations in environmental factors are shown graphically in the papers by Lillick (1937), Clarke and Zinn (1937) and Clarke (1938). Numerical values were read from the curves to be applied to the equation. In several respects the data differed from the Georges Bank survey, occasionally necessitating changes in the method of calculation.

Probably the most significant difference is the fact that the Georges Bank calculation is based on cruise averages and the one for Woods Hole on individual station analyses. Therefore the latter, while it appears to give a very complete picture of the seasonal cycle, undoubtedly contains a certain amount of variation which is not truly seasonal but rather is the result of horizontal movements of variable water masses.

In the second place, the phytoplankton was measured by counting cells rather than by chemical analysis as in the Georges Bank survey. This does not invalidate the application of the equation, since the latter deals with rates of change rather than with absolute quantities. However, the inherent assumption that cell counts are proportional to the total size of the population irrespective of species composition is not fully justified.

In the Georges Bank survey an average seasonal curve was used to obtain radiation values. Clarke (1938) obtained measurements from the Blue Hill observatory, and these are used in preference to the average curve for the area. Clarke also used photometers to measure the extinction coefficient k, which was of course superior to the Secchi disc measurements made on Georges Bank. These values for I_o and k were used to estimate the depth of the euphotic zone z_1, defined as

$$z_1 = \frac{lnI_o - ln\,0.0015}{k}. \qquad (2)$$

In a good many cases, however, z_1 was greater than the actual depth of water at the station (30m.). Therefore, it was necessary to modify the definition of the euphotic zone as follows: z_1 = the depth at which the light intensity is 0.0015 g. cal. per cm^2 per minute, or the total depth of water if the latter is less than the former.

Data on temperature and salinity (Clarke, 1938) show that November and early December was the only time in the year when the waters were mixed to a depth greater than that of the euphotic zone. The correction factor $1 - V$ is therefore relatively unimportant.

Evaluation of the nutrient factor $1 - N$ is based on the average phosphate concentration in the upper 15 m. (mean of analyses at 2 m. and 15 m.). This is preferable to using only surface values, since there appears to be considerable variability at the two levels, which is due to water movements rather than to seasonal fluctuation.

The factors considered up to the present—radiation, transparency, the depth of the euphotic zone, vertical turbulence, and phosphate—are combined in the way indicated in equation (1). The result is the estimated photosynthetic rate of the Woods Hole plankton, shown in the appendix under the heading P_h. The remaining terms in the equation each have a single variable. The respiratory rate varies according to the temperature T. The grazing rate depends on the quantity of zooplankton Z. The latter was collected and measured by methods that are not exactly comparable with those of the Georges Bank survey. On Georges Bank, the zooplankton was caught in a quantitative plankton sampler (Clarke and Bumpus, 1940) using a No. 2 net (22 threads to the cm.), and the volume of plankton was measured by the displacement method. In the Woods Hole area, thirty-minute oblique hauls were made with a 1.5 m. scrim net, and the volume of the catch was measured after settling one month. The scrim net had only ten threads per cm., but the threads were large, so that the pores were not much different from those of the No. 2 net. The efficiency of the net was determined by comparison of the catch with samples taken with a pump. Thus the total quantity of large zooplankton is known with some accuracy, but many forms smaller than Stage IV Calanus were lost through the meshes of the net. The amount lost was probably large, since the authors state that the area produces enormous quantities of young *Pseudocalanus minutus*, particularly during the spring months, and evidence of such an increase does not appear in the scrim net catches. Thus there are two incongruities in the comparison: (a) the Woods Hole survey secured a different and probably smaller fraction of the total zooplankton population, and (b) the volume of plankton was measured by a different method. According to Redfield (1941), settling volumes are three to seven times larger than the displacement volume of the same catch. The two errors appear to work in the opposite directions, but how nearly they balance each other cannot be determined from the available data. As a first approximation it will be assumed that they do, but it will be seen later that the assumption is responsible for considerable uncertainty in the final result.

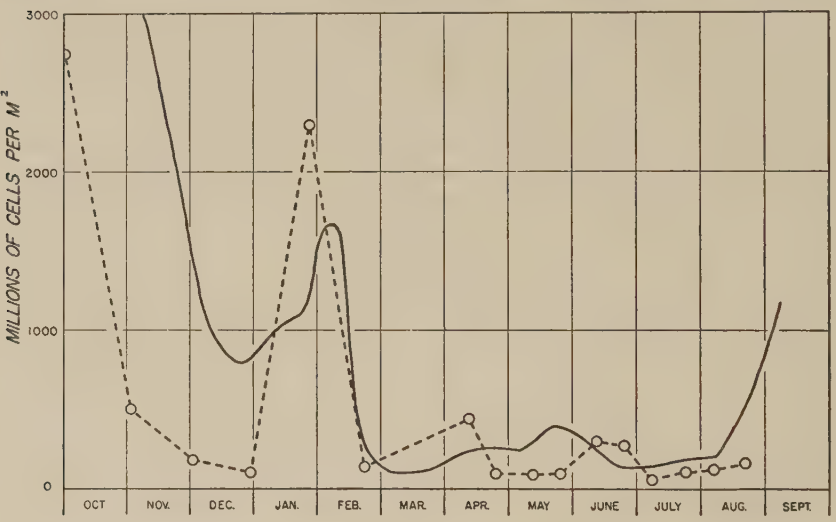

Figure 32. Circles and dotted lines show the seasonal cycle of phytoplankton (millions of cells per m²) in the waters off Woods Hole. Solid line is a theoretical population curve calculated from environmental factors according to equation (1) in text.

The appendix shows the estimated zooplankton crop and the derived values for grazing rates. The final steps in the calculation are (a) the determination of the rate of change of the population by subtracting the respiratory and grazing rates from the photosynthetic rate, and (b) the integration of the rate of change of the population in order to obtain the seasonal population curve. This operation is carried out in accordance with methods previously described (Riley, 1946). The result is shown in Fig. 32, in which the calculated population is represented by a solid line, and the observed number of cells by circles and dotted lines.

DISCUSSION

Fig. 32 shows that a fair degree of success is attained in applying the Georges Bank equation to the Woods Hole survey. Although the agreement between the calculated and observed populations is by no means perfect, the equation properly delineates the major points of difference between the phytoplankton cycles in the two areas. The reasons for these differences will be understood more clearly by examination of Fig. 33, which shows a detailed comparison of the various parts of the two calculations. It is apparent from the figure that no one factor is responsible for the results.

During the midwinter lull in plankton production on Georges Bank there is a long period when a close balance exists between accumulation and dissipation of phytoplankton carbon. This period comes to an end when the establishment of vertical stability increases the photosynthetic rate, and the spring diatom flowering follows. In the waters off Woods Hole, where coastal drainage maintains stability, there tends to be an excess of production over consumption as soon as the vernal increase in radiation begins. Probably a flowering may be expected any time after the first of January and is most likely to occur during a period of bright weather.

The quick cessation of the flowering in both areas is a grazing effect. The lack of subsequent spring flowerings of any size in the Woods Hole area is largely the result of nutrient depletion. Differences in the two seasonal cycles appear to be controlled to a considerable extent by the relative availability of nutrients. The deeper water offshore serves as a reservoir of nutrients that are gradually made available to the surface layer by vertical turbulence during the winter and spring months. Hence the total growth in these waters is greater than it is near shore. On the other hand, in the summertime nutrients regenerated on or near the bottom are from time to time returned to the surface layer in the coastal area, leading to sporadic flowerings during the summer and early autumn, while farther offshore the vertical distribution of nutrients seems to be largely confined to the autumn months when increasing turbulence and decreasing light intensity tend to inhibit a flowering.

A serious objection might be raised to the treatment of the nutrient problem in the Woods Hole area in that phosphate is the only factor considered in the equation. Lillick (1937) believed that nitrate was more important than phosphate in controlling phytoplankton production. This conclusion was based on two observations—first, that the seasonal trend of the nitrate curve was more closely correlated with phytoplankton than was the phosphate curve, and second, that the

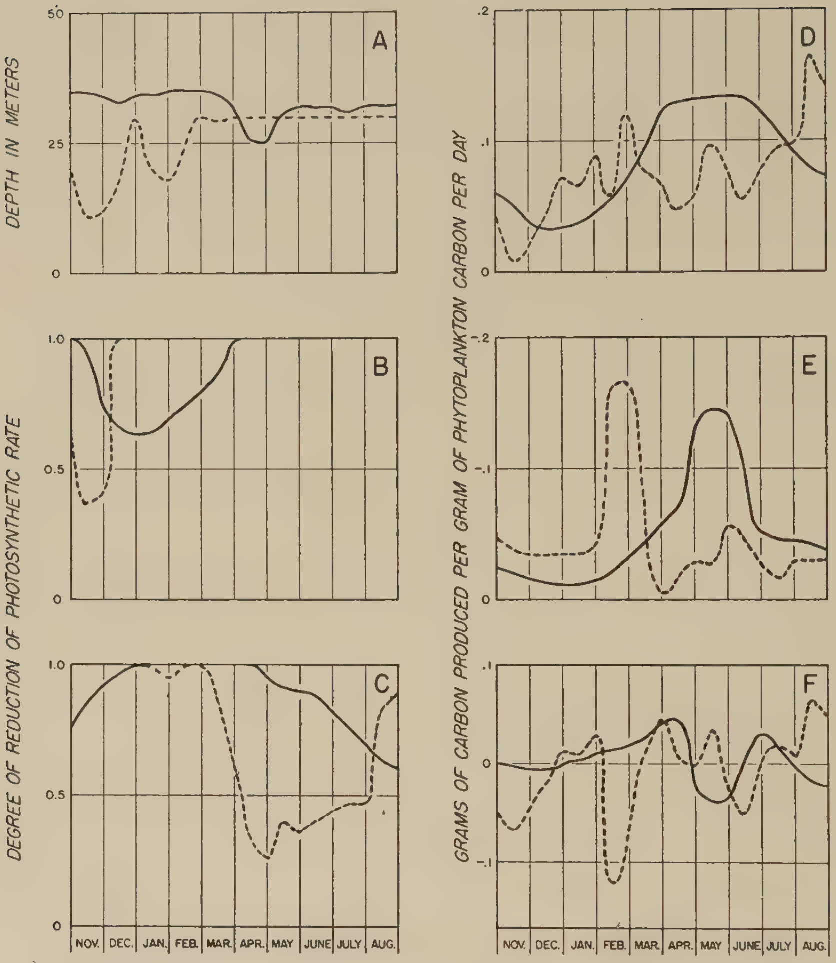

Figure 33. Comparison of environmental factors and phytoplankton growth processes on Georges Bank (solid line) and the Woods Hole area (broken line). A. The estimated depth of the euphotic zone (z_1) based on solar radiation and transparency. B. Reduction in photosynthetic rate by vertical turbulence ($1 - V$). C. Reduction in photosynthetic rate by nutrient depletion ($1 - N$). D. The calculated photosynthetic rate (P_h). E. The calculated grazing rate (G). F. The estimated rate of change of the population ($P_h - R - G$).

nitrate to phosphate ratio was lower than is the normal ratio found in the open oceans. If Lillick's argument is correct, the introduction of a nitrate factor will decrease the average rate of photosynthesis and will therefore change the form of the seasonal cycle. Unfortunately there is no very good quantitative information on the effect of nitrate on the photosynthetic rate. It appeared to be of little significance in the Georges Bank area; moreover, Ketchum (1939) found that 47 mgs. per m^3, the minimum concentration used in his experiments on *Nitzschia closterium*, did not reduce the growth rate. On the other hand Harvey (1933) found a difference in photosynthetic rate between cultures that were very deficient in nitrogen and others which had been enriched to the extent of 60 mgs. per m^3.

This fragmentary information does not lead to the formulation of a precise theory. Suppose, by way of experimentation, that the nutrient factor shall be the lower one of the following ratios: (a) the ratio of the phosphate concentration to 0.55 mg.-atom per m^3, or (b) the ratio of the nitrate concentration to a similar sort of maximum value for the limiting effect of nitrate. The largest value that can be postulated for this limiting effect is 47 mgs. of N per m^3. It will have the effect of reducing the average photosynthetic rate to 56 per cent of its previous value. The effect on the seasonal cycle of the phytoplankton population is shown in Fig. 34, in which the solid line is the crop as previously determined, and the broken line shows the effect of introducing a maximum nitrate factor. If the limiting nitrate concentration were reduced from 47 mgs., the effect on the photosynthetic rate would also be decreased, and at 20 mgs. there would no longer be a nitrate effect. It is evident, therefore, that depending on whatever assumption is made about nitrate limitation, the curves will fall somewhere between the limits drawn. It is also apparent that although the various assumptions alter the goodness of fit of the population curve, it is a skewing effect rather than a change in its essential features. There remains a rapid decrease from an autumn maximum, a late winter flowering, and no spring flowering of any consequence.

Although the original equation is a better fit for the data than the modification that includes a nitrate factor, it would be unfair on this basis alone to discount Lillick's theory of nitrate limitation. There remains the uncertainty of the evaluation of the grazing effect. Perhaps the assumptions on this subject over-rated the importance of small animals that escaped the scrim net. If this were true the estimate of the grazing rate should possibly be reduced to one-third or one-fifth the assigned value. This again skews the phytoplankton population curve and in extreme cases invalidates the comparison. A wide variety of results can be obtained by combining various assumptions

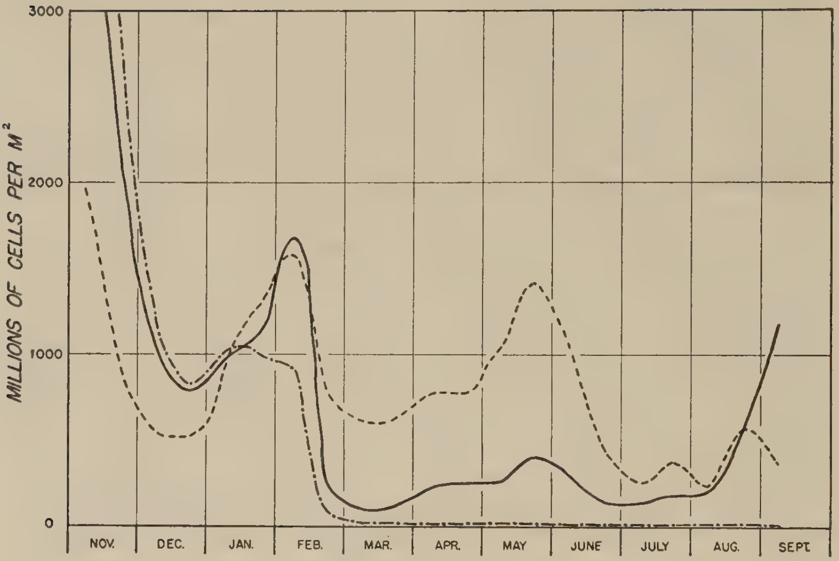

Figure 34. Comparison of different methods of calculating the theoretical population curves. Solid line, direct application of the Georges Bank equation. Broken line, introduction of a factor expressing the maximum possible effect of nitrate depletion. Dotted line, nitrate factor and reduction of grazing factor to one-third.

about the nitrate factor and the grazing effect. One is shown by a dotted line in Fig. 34, in which is assumed (a) maximum nitrate limitation, and (b) reduction of the grazing rate to one-third. It is a good fit for the data except that it postulates a secondary spring flowering in May which is almost as large as the February population. However, this may not be a very significant difference, since the calculation does not make allowance for grazing by the large spring crop of microcalanoids.

The results demonstrate the need for standard methods in regional surveys. Small differences in method may be of little importance in qualitative descriptions, but they assume major proportions as soon as quantitative comparisons are attempted. In the present case differences in methods of measuring the zooplankton in the two surveys are sufficient to prevent exact comparison. The assumptions that are made about this comparison of data determine to a large degree how accurately the Georges Bank equation fits the Woods Hole data. Nevertheless, changing the assumptions tends only to distort the curves rather than to destroy their distinguishing features. In no case does the curve resemble the Georges Bank seasonal cycle.

Therefore the results lend considerable credance to the view that differences in the seasonal cycles in the two areas are caused by rather small variations in the same basic group of six environmental factors. There is no evidence that the New England coastal populations must be explained by special phenomena such as species differences or the influence of land drainage.

SUMMARY

1. Previous studies of the phytoplankton in New England waters have shown that the seasonal cycle in coastal waters differs from that of the offshore banks in respect to the size of the spring flowering and its time of inception, the relative importance of summer and autumn flowerings, and the difference between maximum and minimum populations.

2. The reasons for these differences are investigated by comparing the seasonal cycles of Georges Bank and the coastal waters off Woods Hole. It had been found that the Georges Bank population was susceptible to a mathematical treatment such that seasonal variations in radiation, transparency, depth of the isothermal surface layer, the quantity of phosphate, temperature, and the amount of zooplankton could be combined in an equation which accurately predicted the phytoplankton cycle. The same equation is now applied to the Woods Hole data with a fair degree of success.

3. Certain difficulties are encountered in comparing the two populations because the methods used in the two surveys were not exactly the same. Assumptions must be made about how to convert the two sets of data into comparable terms, and this prevents precise application of the equation. Thus a variety of results is obtained, but in most of them a fair degree of success is obtained in fitting the equation to the data.

4. It is therefore probable that the differences between the observed populations in New England coastal waters and the offshore banks are the result of differences in simple environmental factors—transparency, stability, phosphate, etc.

APPENDIX

Numerical Values Used to Calculate the Rate of Change of the Woods Hole Phytoplankton Population. For Explanation of Symbols See Equation (1) in Text

Date		I_0	k	z_1	$1-V_1$	$1-N$	P_h	R	Z	gZ	P_h-R-G
Nov.	1	.132	.26	19	.63	1.00	.043	.048	6.3	.047	−.052
	15	.035	.33	11	.37	1.00	.009	.039	5.2	.039	−.069
Dec.	1	.094	.36	12	.40	1.00	.021	.032	4.7	.035	−.046
	15	.070	.24	18	1.00	1.00	.041	.027	4.7	.035	−.021
Jan.	1	.122	.14	30	1.00	1.00	.072	.024	4.7	.035	.013
	15	.125	.24	20	1.00	1.00	.065	.021	4.7	.035	.009
Feb.	1	.191	.30	17	1.00	.95	.087	.019	5.3	.040	.028
	15	.104	.18	25	1.00	1.00	.056	.018	21.4	.161	−.123
Mar.	1	.205	.14	30	1.00	1.00	.120	.018	22.2	.167	−.065
	15	.188	.18	29	1.00	.87	.078	.021	6.0	.045	.012
Apr.	1	.243	.18	30	1.00	.62	.069	.023	.4	.003	.043
	15	.205	.12	30	1.00	.33	.047	.023	2.3	.017	.007
May	1	.333	.13	30	1.00	.26	.055	.029	3.7	.028	−.002
	15	.382	.13	30	1.00	.40	.096	.036	3.6	.027	.033
June	1	.312	.13	30	1.00	.36	.082	.046	7.5	.056	−.020
	15	.229	.14	30	1.00	.40	.055	.058	6.4	.048	−.051
July	1	.354	.16	30	1.00	.44	.077	.049	3.6	.027	.001
	15	.320	.13	30	1.00	.47	.094	.061	2.0	.015	.018
Aug.	1	.350	.14	30	1.00	.47	.097	.060	4.0	.030	.007
	15	.343	.14	30	1.00	.82	.165	.068	4.0	.030	.067
Sept.	1	.274	.14	30	1.00	.89	.143	.064	4.0	.030	.049

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Contribution No. 370

A SALINOMETER FOR USE IN BRACKISH WATER[1]

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In principal this salinometer is a "battery" composed of a pair of dissimilar metals immersed in the brackish water of the field as an electrolyte. Between these dissimilar metals there exists a potential difference which is practically independent of the concentration of salts in the electrolyte over a very wide range. However, the salt concentration has a marked effect upon the conductivity of the electrolyte. If the measuring circuit has constant resistance, the only change of resistance in the total circuit is that due to the change of conductivity of the water in which the cell is immersed. Since the driving EMF is essentially constant, the current flowing in the circuit is a measure of the conductivity of the water sample.

The conductivity of salt solutions varies with both salt concentration and temperature, an increase of either quantity in dilute solution producing an increase in conductivity. Fortunately there is a way to neutralize the changes of conductivity due to changes of temperature, leaving only those due to changes of salinity. Aqueous salt solutions have a negative temperature coefficient of resistance while most metals have a positive one. It is a simple matter, therefore, to place in series with the cell and in thermal contact with the water a wire resistor having a positive thermal coefficient and a numerical change of resistance both equal and opposite to that of the water sample. This method of temperature compensation is not exact for all salinities, since the temperature coefficient of resistance of salt solutions changes with the salt concentration, but the errors are small. A midrange salinity can be chosen in accordance with the demands of the field problem and the change of resistance (ΔR) of the cell measured over the range 0 °C., to 30 °C.; (ΔT). Knowing α, the temperature coefficient of resistance for the metal wire compensator, one can calculate the room temperature resistance ($R_{\circ}$) needed to compensate the cell.

$$R_{\circ} = \frac{(\Delta R)}{\alpha\,(\Delta T)}$$

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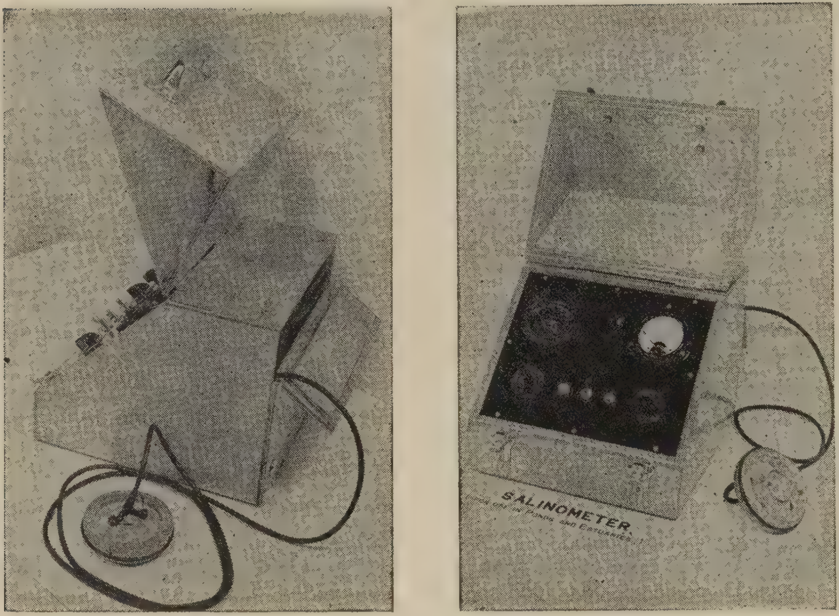

Figure 36. (*Left*)—Side view showing part of 50 feet of cable, underwater unit, and the stowage compartment for both. The temperature compensating resistor winding is on top of the disc-shaped underwater unit. The complete instrument weighs 22 pounds and occupies less than one cubic foot of space. (*Right*)—Front view showing the salinity indicator (white dial), the polarization current indicator (black dial), with the calibration knob between. In the lower bank (left to right) are polarization current limiter, battery switch, salinity indicator switch, reading switch, and the range selector. Note the calibration chart in the lid, as well as the ring electrodes and perforations in the underwater unit.

Nickel wire 0.010 inches in diameter, having an $\alpha = 0.006$ ohms/°C., has been found most suitable. The cell itself can be built of practically any combination of metals or substances susceptible to strong and lasting polarization, such as Carbon. Experiments with many combinations show Copper and Zinc to be electrically and chemically suitable. The physical shape of the Cu-Zn pair is relatively unimportant and may be altered to suit the requirements of the investigation. A problem presented to the writer was the measurement of the salinity of thin layers of terrigenous fresh water floating on, and mixing with, sea water in a small estuary which was being used for ecological studies (Edmondson, 1947). The electrode shape finally chosen was a pair of concentric horizontal rings a few millimeters in height. These, together with a flat ring of lucite on which the compensating resistance wire was wound, produced a cylindrical underwater unit

1 cm. high and 10 cm. in diameter which was so thoroughly pierced with large holes that it disturbed the water only slightly when lowered through the boundary between stratified water layers. Through efforts to maintain lowest possible cell resistance, it was found that twice as much Zinc surface as Copper surface was needed. For this reason the outer ring was made of Zinc and the inner one of Copper.

This ratio of areas is also found to be best in the case of flat plates. Long narrow plates are more efficient than square ones. Efficiency is gauged in terms of the largest current passed through the measuring circuit when comparing electrodes of the same area and spacing but different shape. Long narrow electrodes also have the least "surface error": specifically, a reduction of current in the measuring circuit due to the electrodes being quite near the liquid surface boundary across which the ion field cannot develop. Electrodes having an aspect ratio greater than 10 to 1 can be brought within 0.5 of a ratio unit of the surface before surface effects become serious. This is less than the practical limit, since the temperature compensator is then out of water.

The preparation and use of Copper-Zinc electrode pairs involves a simple preliminary technique. A new Copper-Zinc electrode pair immersed in a saline solution develops an EMF instantly, but the current flowing between the plates is subject to rapid change, ultimately subsiding to a vanishing quantity. This is due to the insulating effects of the reaction products on the plates through which most of the initial potential drop is eventually consumed. To avoid this effect an outside EMF, larger than that of the cell, is applied to drive the cell backward producing a copious emission of bubbles (H_2) at the Zinc plate. Thirty seconds of treatment at one ampere prepares the electrodes for use. During the counter polarization treatment a number of compounds are developed on both electrodes (Bengough and May, 1924). The Zinc electrode is oxidized and eventually develops a white coating of $ZnCO_3$ upon exposure to air. The Copper electrode at first becomes yellow with $CuCl_2$, Cu_2O and, in the presence of sufficient oxygen, $Cu_4(OH)_6Cl_2 \cdot H_2O$, turning yellow-green and finally blue-green upon exposure to air. The final coating is mossy or slightly botryoidal, its color being determined by the preponderance of Malachite $CuCO_3 \cdot Cu(OH)_2$ [the basic Cupric Carbonate developed in the presence of atmospheric CO_2], and Cupric Oxychloride $CuCl_2 \cdot 2\,CuO \cdot 4\,H_2O$.

After preparation the behavior of the electrodes is quite changed, as is shown in Fig. 37. Upon immersion in the water sample the current at first falls off rapidly, then more slowly, and finally, in a matter of 10 seconds all told, it assumes a constant value which is maintained for several minutes before beginning the asymptotic decline toward

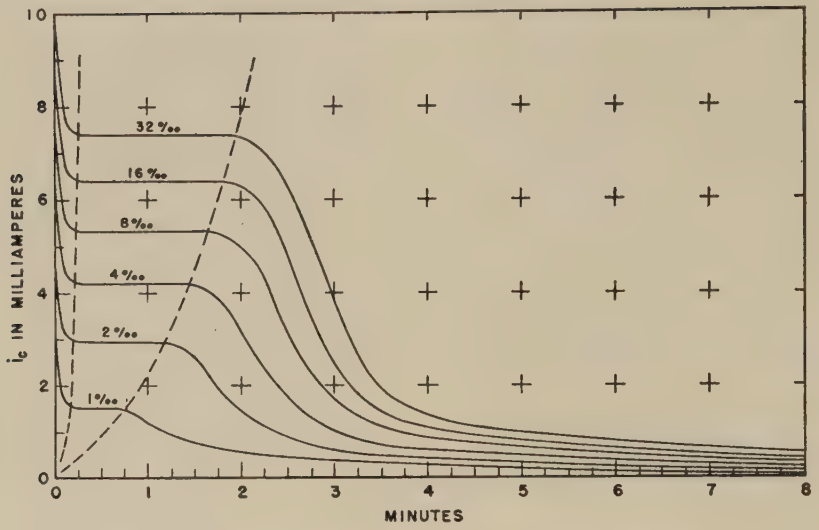

Figure 37. Current Variation with Time at Different Salinities.

zero. The plateau value is the one which is useful in salinity measurement. It is thought that this plateau is produced by the slow solution of the chemical products of counter-polarization. The plateau lasts longer in high salinity water than in low, suggesting that the rate of solution is controlled by the concentration of salts around the electrodes. Counterpolarization is complete when the current output of the electrodes, immediately after recharging, has a plateau in its time rate of decline. The plateau results from a certain number of coulombs of charge having been passed backwards through the cell. The length of the plateau in time is not conspicuously increased by an overdose of charge but the time required for the plateau to be reached is measurably increased. For this reason it is helpful to place an ammeter in series with the counterpolarizing EMF. Its reading is at first 10 per cent higher than later, a sudden drop indicating when the counterpolarization process is complete.

The salinometer circuit, including that of the underwater unit, is given in Fig. 38. The principal control is the "reading switch," a double-throw, single-pole switch that automatically cuts out the salinity-indicating milliammeter whenever the counterpolarizing current is cut in. Calibration is accomplished by means of a variable resistor in series with the salinity indicator. A bottled sample of water of known salinity must be carried along for calibration purposes. After the underwater unit has been counterpolarized for a minute or so to

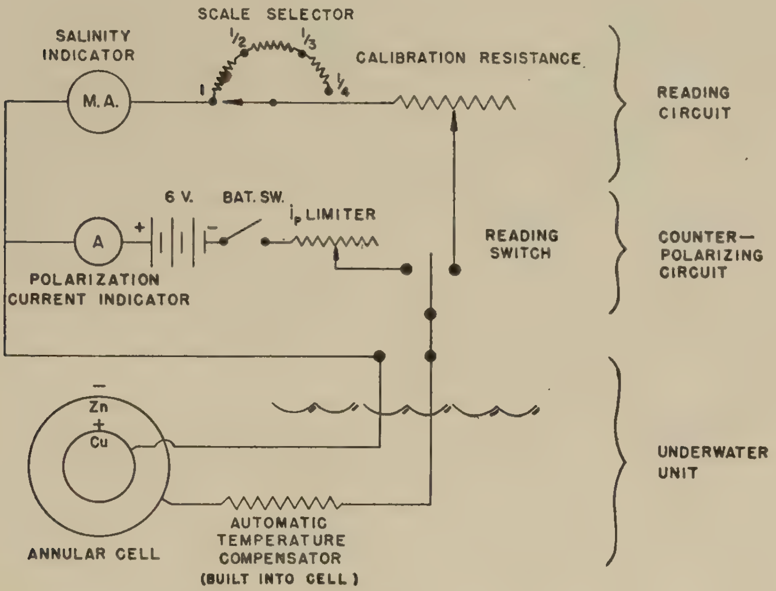

Figure 38. Salinometer Circuit Diagram.

insure the restoration of the deposits on the electrode surfaces and their thorough saturation with water, the reading switch is thrown and the system is allowed to come to equilibrium in the calibration sample. By adjustment of the resistance of the reading circuit the milliammeter can be made to read properly the salinity of the known sample based upon the original calibration curve made in the laboratory from a series of other known samples. In the field, calibration at only one point is sufficient to bring the whole scale of values into proper alignment. Recalibration is desirable every now and then to be sure that mechanical shifting caused by inadvertent bumping of the instrument, or the sun's heat, has not changed the preliminary calibration.

The calibration curve for the instrument is exponential in appearance, but it follows no true exponential function as far as is known. A family of such curves for different temperatures is shown in Fig. 39. These curves were determined by cutting a sample of sea water of prearranged temperature and known salinity with fresh water at the same temperature, counterpolarization having been standardized at 15 seconds and applied before each reading. The cuts were made in the ratios 1/1, 1/2, 1/4, 1/8, 1/16, 1/32, these being successive cuts each by

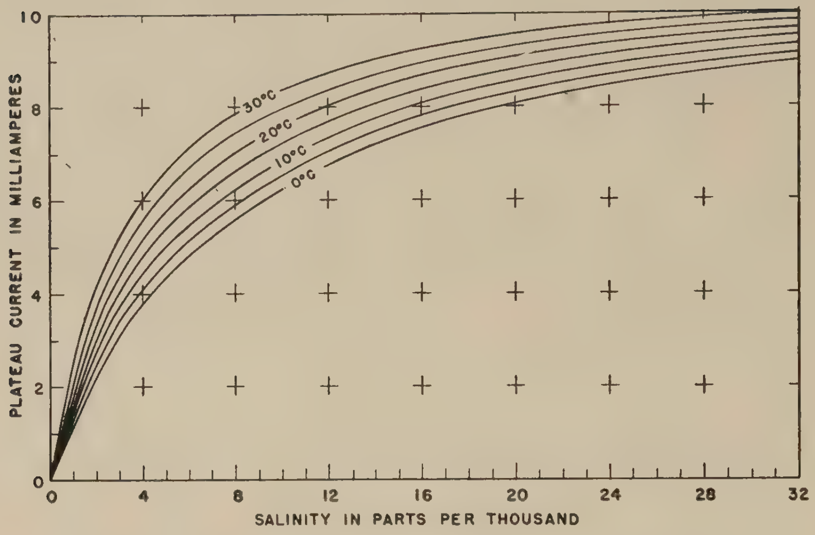

Figure 39. Characteristic Calibration Curves for Various Temperatures.

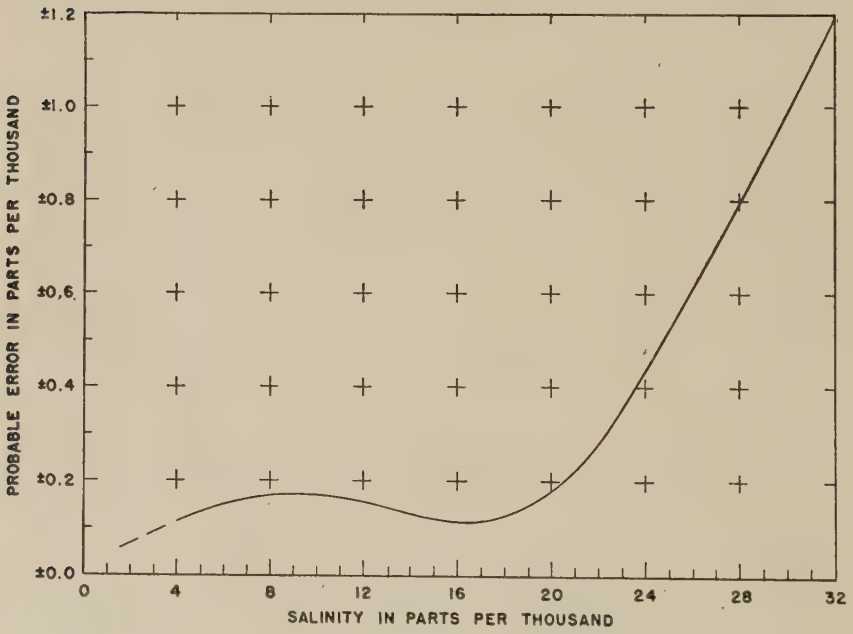

Figure 40. Residual Errors Including Reading Error After Temperature Compensation at 20° C. and 16°/oo.

half of an original volume. With a temperature compensated cell only one or two such runs need be made, and these without excessive attention to temperature. It will be noted that the shape of the calibration curve is such that the accuracy of measurement increases as the salinity diminishes. In addition to this scale convergence there is a milliammeter reading error of approxiamtely ± 2 per cent of the full scale deflection which arises in part from the error of the eye in reading the meter and in part from errors in the reproducibility of the pointer movement itself. These errors, together with those remaining after temperature compensation, are given in Fig. 40, which assumes the temperature error to be zero at 20° C.

Of the salinometers in use at present, this salinometer is less accurate and more sensitive to temperature than others. But it has the great advantage of portability, which, together with its simplicity, wide range and ease of calibration, makes it useful for programs of work where the salinity gradients are large and abrupt, or where it is desirable to measure the initial thickness and mixing zones of excessively thin layers of water. It is also inexpensive to build and maintain.

Mr. T. Wehe has earned the writer's gratitude for his painstaking assistance in making repeated thermal calibration runs and experiments with a large variety of electrode sizes and compositions.

SUMMARY

The salinometer is a simple electrical instrument for direct measurements in the field of a wide range of salinities. It is particularly well suited for use from a skiff, since it is light, portable and readily calibrated in the field. Because the approach is simpler, the instrument is described in terms of empirical relationships between the experimental variables rather than rigorously in terms of physical chemistry. From the experimentally derived curves the behavior of the instrument can be predicted sufficiently well for purposes of design and readaptation to special investigations.

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Contribution No. 371

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DECOMPOSITION AND REGENERATION OF NITROGENOUS ORGANIC MATTER IN SEA WATER.* VI. THE EFFECT OF ENZYME POISONS

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When organic matter, in the form of natural marine plankton, is allowed to decompose in sea water in the dark under laboratory conditions ammonia is first found in the water, followed by nitrite, and later by nitrate, in amounts corresponding to the nitrogen which disappears from the suspended particulate matter. When, in the last stage, the water is inoculated with fresh diatoms a new flowering takes place in the light, with the disappearance of nitrate from the water. In darkness, this new organic matter again decomposes and the cycle repeats itself. Many of the features of this cycle, and the effects of such variables as time, temperature, source of water and organic matter, etc., we have reported in previous papers (1937–1942).

To renew these studies, after an enforced delay of three years, we chose to investigate the effects of certain enzyme poisons on the several stages of the decomposition and regeneration cycle. The plan was to start decomposition "cultures" consisting of natural sea water and marine phytoplankton material and to follow the ammonia and nitrite in the water, in control portions as well as in portions to which enzyme inhibitors were added at various stages in the cycle.

Since the effects to be observed were at most semi-quantitative it was possible to simplify the analytical techniques to reduce the laborious character of the ammonia analyses and to eliminate the determination of nitrate and particulate nitrogen. The distillation procedure for ammonia was identical with that previously described, but after collecting the distillate the ammonia in it was finally determined by Nesslerization rather than by titration with hypobromite. While not as accurate, this procedure was sufficient for the purpose and more rapid. Nitrite was determined by the same colorimetric method as before, with the use of the Klett-Summerson photoelectric colorimeter in the later stages of the work.

EXPERIMENTAL

Four decomposition "cultures" were prepared (Nos. 101, 103, 104, and 105) from water obtained in Vineyard Sound near Woods Hole. Phytoplankton was collected in a double net, so that the larger organisms were eliminated. The tow consisted principally of *Rhizosolenia.* Varying, undetermined quantities of this material were added to the water in 5-gallon carboys, No. 104 containing the largest amount and No. 103 the least. Smaller portions (about 2 liters) were removed to separate containers and the inhibiting substances added in fixed concentrations. These were allowed to decompose in the dark, at laboratory temperature, simultaneously with the main "control" portion of each culture. At intervals, determinations of ammonia and nitrite were made and at certain times portions were again removed from the main culture and inhibitors were added.

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* Contribution No. 371 from the Woods Hole Oceanographic Institution.

The enzyme poisons used were: KCN, in concentrations from 0.0001 to 0.01 M; NaF, 0.01 and 0.03 M; As_2O_3, 0.01 M; sodium iodoacetate, 0.01 M; ethyl, propyl and *n*-butyl carbamates, 0.2 M. These were rendered neutral by addition of acid or alkali as required and were added at various stages in the cycle: at the beginning; when the ammonia had reached a maximum; and when the ammonia had been entirely replaced by nitrite.

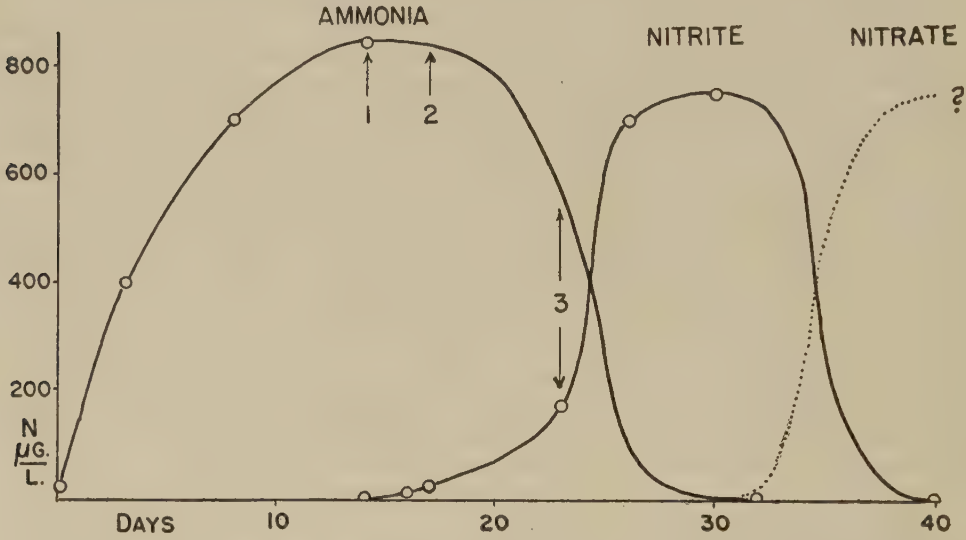

FIGURE 1. Series No. 104. Formation of ammonia, nitrite (and nitrate by inference) during decomposition in the dark. Source of organic matter, principally *Rhizosolenia* suspended in water from Vineyard Sound. Time in days, nitrogen in micrograms per liter. At points indicated by *1, 2,* and *3* portions of this control culture were removed and to them were added various enzyme poisons, as described in the text.

Figure 1 shows the course of the cycle in Series 104. In the control, ammonia reached its maximum after about 15 days, at which time nitrite was first detected. The latter reached its maximum about 15 days thereafter, and in another 10 days—or 40 days from the start of the decomposition—it had again disappeared entirely. We know from previous experience that complete oxidation to nitrate has taken place at this time. At the beginning of the experiment five 2-liter portions were removed, to which were added respectively: *A*, KCN, 0.01 M; *B*, KCN, 0.001 M; *C*, KCN, 0.0001 M; *D*, NaF, 0.03 M; *E*, As_2O_3, 0.01 M. At the point marked *1* in Figure 1, at 14 days, portions were removed to which were added: *F*, KCN, 0.01 M; *G*, KCN, 0.001 M; *H*, As_2O_3, 0.01 M. At point *2*, at 17 days, similar sub-cultures were prepared containing: *J*, ethyl carbamate, 0.2 M; *K*, propyl carbamate, 0.2 M; *L*, sodium iodoacetate, 0.01 M. At point *3*, sub-cultures were prepared containing: *M*, KCN, 0.001 M; *N*, KCN, 0.0001 M.

Series 101 and 103 were carried out in the same manner, except for variation in the times at which the inhibitors were added. Series 105 was carried through the first half of the cycle only, to learn the effects of the carbamates and of iodoacetate on the liberation of ammonia.

RESULTS

The results and conclusions are based upon observation of the relative rates of appearance and disappearance of ammonia and nitrite in the presence and absence of inhibitors. The graphic details of these experiments need not be reproduced, but the following observations were made as to the specific effects of the various poisons.

KCN

In no case did significant amounts of nitrite appear in any culture to which KCN was added, even in concentrations as low as 0.0001 M. When KCN was added, even in the lowest concentration, to cultures in which nitrite had already appeared, the latter did not increase in amount, showing that the oxidation of either ammonia or nitrite was inhibited. In 0.0001 M concentration it had no effect upon the formation of ammonia, but in concentration of 0.001 or 0.01 M it greatly retarded the rate. In Series 104, for example, in which ammonia had disappeared in about 30 days in the control culture, less than half the maximal amount had appeared in 46 days in the presence of 0.01 M KCN.

Carbamates (ethyl, propyl, n-*butyl)*

When carbamates were added in 0.2 M concentration to cultures already containing ammonia no nitrite formed. If nitrite had already appeared before carbamate was added it did not further increase. Carbamate therefore appears to inhibit the oxidation of both ammonia and nitrite. It was not possible to determine the effect of carbamate upon the formation of ammonia since it interfered with the analysis, decomposing during the distillation and also rendering the Nessler reagent inactive.

Iodoacetate

Iodoacetate inhibited both the formation and further oxidation of nitrite, exactly as cyanide and carbamate. A single experiment indicated that it permitted the formation of ammonia, but somewhat more slowly than in its absence.

NaF

In a concentration of 0.03 M sodium fluoride did not interfere with ammonia formation, but in this concentration, as well as in 0.01 M, it prevented oxidation to nitrite. It should be mentioned, however, that these concentrations produce a copious precipitate of CaF_2, so that the resulting concentration of fluoride ion is considerably smaller. The solid precipitate itself may also be a disturbing factor.

As_2O_3

Nitrite did not appear when As_2O_3 was present. Its effect upon ammonia formation was inconclusive; in one case ammonia appeared but in another it did not. It proved difficult to keep the solution neutral, however, and in at least one case a strong acid condition developed which was not detected until the close of the experiment.

Discussion

Microorganisms may produce ammonia through various chemical mechanisms: hydrolytic deamination, reductive deamination and oxidative deamination (Waksman, 1932). Depending upon conditions (for example, aerobic or anaerobic surroundings) and the species of microorganisms present one or the other process will predominate. It is consequently not surprising that variations in the response to inhibitors should occur, since the various mechanisms will involve different enzyme systems. The different response to As_2O_3 observed in two series of the present study can be easily understood on the assumption of the presence of different microbial floras. The non-interference of this poison with ammonia production in one of the series is not surprising; it has been found that the deamination of amino acids by kidney slices proceeds also in the presence of arsenite (Krebs, 1933). There is also a parallel to the ineffectiveness of iodoacetate; Geimann (1936) reports that it does not suppress the ammonia formation within the tissues of the medusa *Aurelia.*

The fact that cyanide retards, but does not completely suppress, ammonia formation is of interest. It is known that all cases of oxidative bacterial deaminations so far studied are inhibited by 0.005 M KCN (Stephenson, 1939). Our observations may therefore be taken to indicate that under normal conditions oxidative deaminations occur and predominate in decomposing plankton samples. They are probably catalyzed by heavy metals. In our cyanide-inhibited samples ammonia formation would then be due to one of the other mechanisms. We cannot decide at the present time whether the slower rate of ammonia formation is due to a weakly developed alternate mechanism in the same bacteria whose oxidative deamination mechanism has been inhibited. It is perhaps just as likely that such organisms have been more or less completely eliminated and that a longer time is required to build up a bacterial population capable of liberating ammonia from protein or its higher decomposition products by a mechanism that is not sensitive to cyanide.

While the production of ammonia is common to many groups of bacteria the formation of nitrite and nitrate is restricted to specialized types. Meyerhof (1916a and b; 1917) studied the metabolism of soil nitrifiers belonging to the two groups involved. He found that both are sensitive to urethanes and that the nitrate formation is also inhibited by cyanide, but he did not study the effect of cyanide upon the nitrite-forming flora. The present study confirms these observations from the corresponding floras occurring in the sea and also establishes the cyanide sensitivity of the ammonia-oxidizing flora.

The action of cyanide can very likely be ascribed to an enzymatic inhibition. This is indicated by the observation that even very small concentrations of this poison can suddenly interrupt both the nitrite and nitrate formation; i.e., inhibition takes place even when the floras have already been built up. One is not dealing, therefore, merely with suppression of the development of the necessary number of microorganisms.

It seems likely that the formation of both nitrite and nitrate is catalyzed by heavy metals. It is possible that the cytochrome system is involved. This seems to follow from the fluoride inhibition. It has been shown in a variety of biological materials that fluoride attacks the cytochrome system; the actual point of attack seems to be cytochrome *c*, rather than the cytochrome oxidase itself (Borei, 1945). It would be of interest to study more fully the possible role of the cytochromes during nitrite and nitrate formation.

Iodoacetate and arsenite, in the concentrations employed, are primarily dehydrogenase inhibitors. The inhibition of nitrite and nitrate formation by these poisons seems to indicate that enzymes of this type are also involved. It is, of course, a well established fact that both oxidases and dehydrogenases are frequently linked in one chain and that both are necessary to complete an oxidative process.

The inhibition observed in the presence of carbamates would under ordinary circumstances strengthen the assumption of the participation of dehydrogenases, since these narcotics are usually considered as dehydrogenase inhibitors. However, in the present case one must be cautious in interpreting the results. It is a well established fact that many organic compounds are definitely toxic to nitrifiers, especially in high concentrations (Meyerhof, 1916b; Fred and Davenport, 1921). For the present, therefore, we cannot rule out the possibility of a non-specific action of the carbamates.

A practical outcome of the present study is the suggestion that cyanide, in exceedingly low concentrations, may be an effective preservative for sea water before analysis for nitrite and nitrate. Various points, however, such as the minimum concentration of cyanide, the time limits of protection, etc., must be studied before it can be recommended for routine use.

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Contribution No. 372

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PATTERNS IN POND ICE

By Alfred H. Woodcock and Gordon A. Riley
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(Manuscript received 31 December 1946)

A curious cell-like partitioning of pond ice excited the interest of the first author during the course of a research project of the United States Navy. Fig. 1 is an aerial view illustrating the partitioning. The same phenomenon has been reported by Brunt (1946), but the authors are not aware of any other published accounts. The purpose of this note is to present observations of the phenomenon and to discuss briefly the underlying mechanism.

On 28 February and 1 March, 1946, these cell-like ice formations were seen on a great many ponds throughout the length of Long Island, New York, and along the coastal regions of the states of Connecticut and Rhode Island. However, some ponds did not exhibit the effect.

The convex appearance of some of the cell-like areas is probably due to a varying intensity of whiteness of the ice. The solar altitude was about 41°, and the azimuth was such as to preclude the possibility that the shadowing effects resulted from actual elevation of the ice.

The dark, elongated areas originating at some of the cell centers are probably open water. They are presumed to be due to wind-wave erosion, which in each case would naturally start in the open water at the cell centers. The long axis of these areas, bearing about 300° true, is probably parallel with the direction of the wind that formed them.

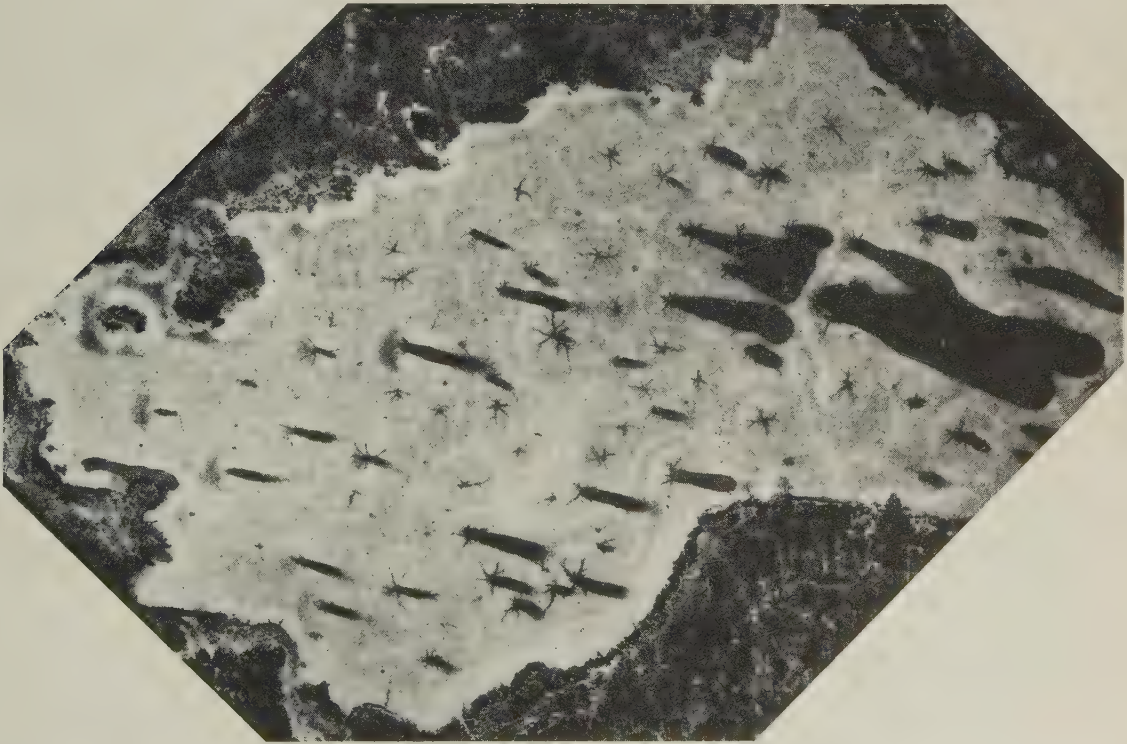

FIG. 1. Vertical photograph of ice-covered Grass Pond on 1 March 1946 from an altitude of 303 meters. The pond is located at lat. 40°53′00″N, long. 72°49′56″W, near River Head, Long Island, New York. North is toward the top of the page. The length of the pond on the east–west axis is 230 meters.

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[1] Contribution No. 372.

The pond shown in fig. 1 was subsequently located from the ground on 14 September 1946. Water depth along three lines of soundings was 57 cm (±3 cm). The following additional notes were made at that time:

Inflow or outflow.—There was no readily visible flow of water to or from the pond.

Pond level.—Measurements of the height of clumps of vegetation identified in fig. 1 lead to the conclusion that the surface of the pond was not more than 36 cm higher on 1 March than on 14 September. It is unlikely that the surface was lower, because there was a rapid thawing of the snow cover during several days preceding 1 March.

The patterns that have been described suggest the existence of thermal convective cells under the ice. There is an extensive literature concerning convective cells set up experimentally in various fluids made thermally unstable (Bénard, 1900; Brunt, 1925; Chandra, 1938). These experiments have shown that, in the absence of general lateral flow, polygonal circulation patterns always occurred when sufficient thermal instability was maintained. Theoretical studies of these motions have been made by Rayleigh (1916), Low (1925), and Pellew and Southwell (1940).

There is a striking resemblance between the experimentally produced polygonal convective patterns and the observed ice patterns. Experimental cells (produced by Bénard, 1900, and others) were set in motion by heating the fluids from below. It is suggested that heating at the bottom of the pond shown in fig. 1 caused water motions which etched their pattern in the overlying ice by producing unequal melting.

Heating of lake water under ice has been shown by Fitzgerald (1895) and by Birge, Juday, and March (1927), who explain it as resulting from a flow of earth heat at the bottom and from absorption of solar radiation penetrating the ice cover.

Successive stages in the thermal history of the pond are suggested in fig. 2. The probable condition when the ice formed is assumed to be a uniform temperature of 0C, represented by the left-hand dashed line. In the next stage, warming at the bottom stabilizes the lowest layer until the temperature reaches 4C. Further heating decreases the density, releasing buoyancy forces which cause the bottom water to penetrate the stable layers above. Eventually the temperature of most of the water mass is raised to a point sufficiently above 4C so that mixing at the upper boundary of the isothermal layer produces water denser than that below. This is the condition (represented by the solid line in fig. 2) thought to exist while the differential melting occurs. The mixing region along the boundary between the stable and unstable water layers is thus brought up to a point just below the ice, so that further mixing produces melting by raising the temperature of the water in contact with the ice. Updrafts of unstable warmer water are marked by excessive melting of the ice; open water eventually appears in the centers, radiating lines showing where lateral divergent flow is producing continued melting. Eventually cooled by this process the water sinks, establishing a closed circulation characteristic of convective cells.

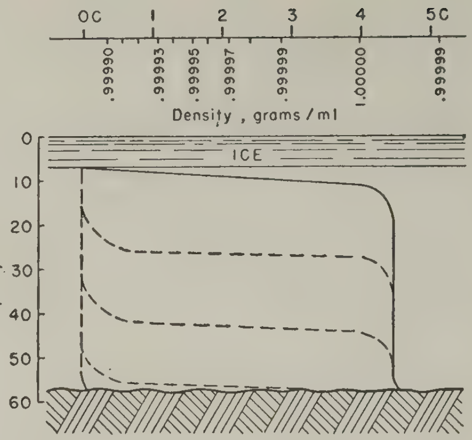

FIG. 2. Suggested vertical distributions of temperature and density.

Bénard (1900) and others have shown that, in experimental convective cells of polygonal form, the cell width is about three times the depth of the fluid layer. The patterns shown in fig. 1 were spaced at distances of ten to thirty times the probable depth of the water. Thus, if these patterns in ice result from convective cells in the underlying water, a different geometrical relationship is indicated.

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TEMPERATURES OBSERVED NEAR THE SURFACE OF A FRESH-WATER POND AT NIGHT

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(Manuscript received 17 February 1947)

The purpose of this note is to present seven sets of vertical temperature soundings made within about one meter of the surface of a pond at night when the air was considerably colder than the water. Large positive lapse rates of temperature were indicated in both the air and the water close to the surface. This information may be of some interest and use to those engaged in boundary-layer problems. Measurements of the cooling of a water surface have been made before [1, 2] but were not so detailed.

Jenkins Pond, where the measurements were made, is located about three miles north of Falmouth on Cape Cod, Massachusetts. The surrounding terrain is very gently rolling and covered with young trees.

The soundings were made at a point about seven meters off the shore from which the wind was blowing. The depth of water at this point was about 70 cm, the maximum that could be reached by wading out in hip boots. The shore had recently been leveled and sand-covered, so that the bottom was very even.

On some of the evenings when these measurements were made, air from the neighboring woods at almost freezing temperature was flowing out over the pond. The water in the pond was about 15C warmer than the air. A layer of fine mist commencing at the edge of the pond varied from 1 cm to 50 cm in height at the point of observation and increased rapidly in thickness in the direction of the air flow. The pond appeared to be 'steaming.'

The temperatures were taken by means of a pan thermometer made by Richter and Wiese. These thermometers are mercury filled; their bulbs are greatly elongated, 10 cm long and 0.15 cm in diameter and inclined at an angle of 45° to the plane of the scale.

The thermometer was clamped, with the bulb horizontal, to a dowel rod which was in turn attached vertically to the fine adjustment of a microscope stage. The thermometer bulb could be raised and lowered by means of the microscope screw. Depths near the surface were measured by using the vernier scale on the fine adjustment, greater heights or depths by using a millimeter scale. The entire apparatus was mounted on a wooden stake which was driven lightly into the sandy bottom.

Whether the thermometer bulb was level was tested by bringing it up from below until it produced a small distinct distortion of the surface. This distor-

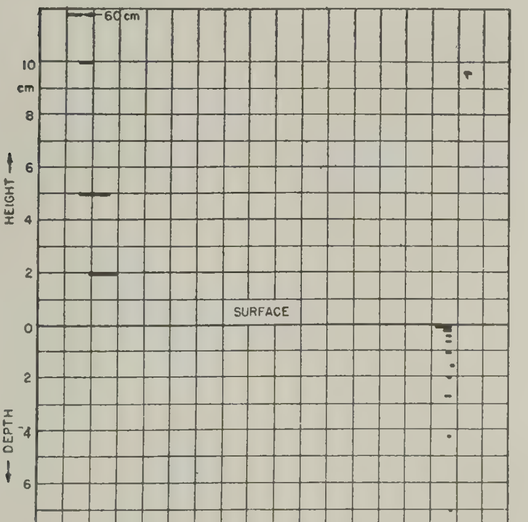

FIG. 1. Temperature sounding, 21 Oct. 1946, 21^h30^m–22^h45^m; sky clear; wind 0.6 m/sec and air temperature 1.3C dry, 0.9C wet at 2 m above the surface; pond slightly steaming.

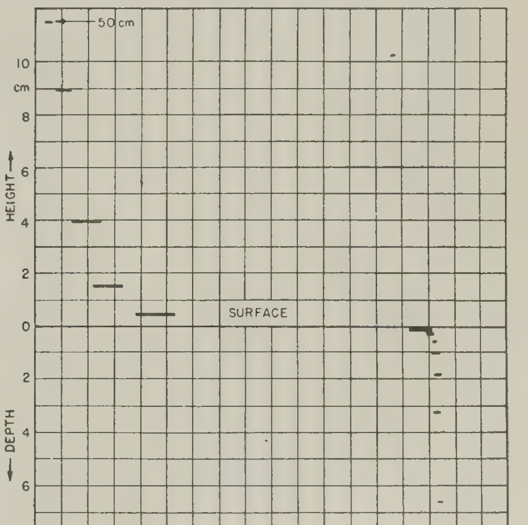

FIG. 2. Temperature sounding, 22 Oct. 1946, 21^h15^m–22^h45^m; sky clear; wind 0.4 m/sec and air temperature −0.3C dry, −0.7C wet at 2 m above the surface; pond steaming.

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[1] Contribution No. 373.

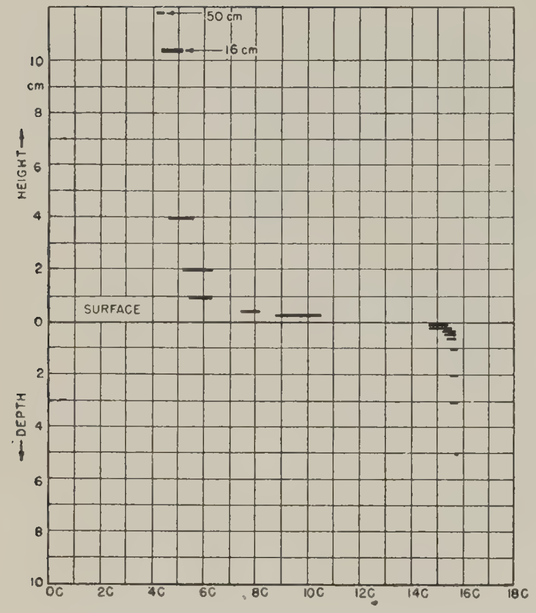

FIG. 3. Temperature sounding, 23 Oct. 1946, $21^{h}17^{m}$–$22^{h}15^{m}$; sky clear; wind 0.8 m/sec and air temperature 4.0C dry, 3.6C wet at 2 m above the surface; pond steaming.

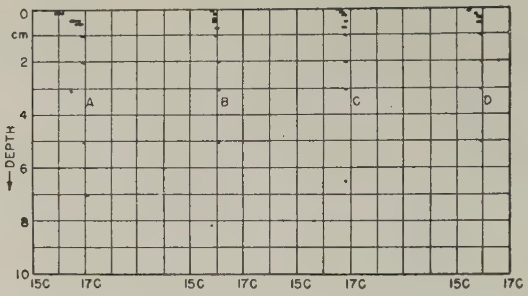

FIG. 4. Temperature soundings in water only: (A) 15 Oct. 1946, $20^{h}30^{m}$–$21^{h}00^{m}$; sky clear; wind 0.6 m/sec and temperature 3.2C dry, 2.7C wet at 2 m above the surface; pond steaming. (B) 24 Oct. 1946, $21^{h}50^{m}$–$22^{h}13^{m}$; sky foggy, no stars visible; wind 0.2 m/sec and air temperature 12.2C dry, 12.2C wet; no steaming. (C) 27 Oct. 1946, $21^{h}00^{m}$–$21^{h}46^{m}$; sky clear; wind 0.1–0.2 m/sec and air temperature 16.3C dry at 10 cm; no wet-bulb temperature taken; no steaming. (D) 1 Nov. 1946, $21^{h}46^{m}$–$22^{h}34^{m}$; air temperature 10.6C dry, 8.6C wet at 2 m.

tion could be easily viewed with a flashlight's reflected image. When the mercury bulb produced a uniform slight distortion over its entire length, it was regarded as satisfactorily level.

Temperature readings were made visually over a period of one minute at each level. No reading was perfectly steady. The limits of fluctuation were recorded in each case; they are indicated in the accompanying graphs by the ends of the little black blocks which represent the temperature soundings. Moreover, the range of altitude corresponding to each reading is equal to the diameter of the bulb and is indicated on the graphs by the vertical thickness of the black blocks.

In only three cases are detailed soundings in both the air and water available. In the other four cases, soundings were made in the water only. The pertinent data for each of the soundings are included in the legends beneath each graph.

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Contribution No. 374

THE BASES FOR TEMPERATURE ZONATION IN GEOGRAPHICAL DISTRIBUTION*

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INTRODUCTION

Zonation, as the term is employed here, refers to the limited north-south distributions which characterize most species. It is well known that these restricted distributions are to be interpreted largely or wholely in terms of temperature. In this contribution an attempt will be made to bring together the main points of our understanding of the relations between zonation and temperature, and to outline the system of logical generalizations which appear to follow from that knowledge. Attention will be confined to the fundamentals of the problem, leaving for a later discussion various matters of detail commonly encountered in particular cases.

I should like to express my appreciation to a number of friends and colleagues with whom this synthesis was discussed during its formative stages, and who contributed many helpful suggestions and comments. Particular thanks are due to Dr. A. C. Redfield, Dr. B. H. Ketchum, Dr. T. A. Stephenson, Professor J. E. Harris, Dr. E. S. Deevey, Jr., and Dr. I. M. Newell. Miss Grace Winter and Miss Margaret Scharff have assisted in the compilation of data, and Miss Scharff has prepared the maps and figures.

THE FUNDAMENTAL BACKGROUND

Investigation has indicated increasingly that zonal distribution boundaries must be correlated with winter or summer seasonal conditions. Dana (1890), Orton (1920), Appellöf (1912), Runnström (1929, 1936), Setchell (1893, 1915, 1917, 1920, 1920a, 1922), Schmidt (1909), and Parr (1933) are among those who have given particular impetus to such considerations in marine biology. Similar ideas have been developed, of course, regarding terrestrial forms, and the same sort of relationships to temperature apparently underlie the zonations of terrestrial and marine species alike. The concepts outlined below, therefore, are valid for either medium. Since this symposium is concerned with marine ecology, however, the discussion is confined to shallow water marine species.

The appreciation of the importance of seasonal temperatures in the control of distribution has emphasized two general types of relationship. In the first of these the dispersal of forms is checked where temperatures become too extreme for survival of the individuals. In the case of a species spreading toward the poles an extreme temperature of this sort is encountered first as a winter temperature. The boundary comes into being where the species is subject to winter killing. For a species spreading toward the equator the comparable boundary arises where summer temperatures first become too high, and dispersal is checked by inability of the individuals to survive the excessive heat. The classic illustration of a marine distribution regulated in this general fashion is provided by the reef corals, apparently unable to survive where temperatures fall below about 70° F. at any time during the year, and accordingly confined within the tropics by poleward winter boundaries of this intensity. The interpretation seems to have been advanced first by Couthouy (1844), and was extended and popularized particularly by Dana (1890).

The second sort of relationship to temperature stressed in distributional studies involves the critical temperatures necessary for reproduction or completion of life cycles. In such cases species spread toward the poles as far as summer temperature conditions are adequate, and towards the equator as far as requisite low temperatures can be obtained in winter. A number of critical phenomena may lead to boundaries of this type, among them trigger temperatures necessary to induce spawning, and growing seasons of adequate duration as well as intensity. Frequently it appears that a critical temperature is directly concerned with the process of reproduction, as in the case of the sponges and oysters studied by Orton (1920) and others. Often, again, the critical temperature is apparently to be sought in a larval stage, or at metamorphosis in sessile attaching forms. Thorson (1946) has recently reviewed evidence of a number of such phenomena. Boundaries depending on adequacy of the growing season—i.e., summer toward the north—are fairly well known. Setchell's (1920) studies on *Ascophyllum nodosum* and other algae whose reproductive or fruiting periods shift into the winter in the southern parts of their ranges may be cited as marine examples showing a comparable importance of winter temperatures for equatorward boundaries.

The important conclusion to be drawn from all such investigations is that distributions may be limited both toward the poles and toward the equator by tolerances or requirements which can be referred either to summer or winter seasonal conditions.

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There is considerable force of logic to this view. Distributional boundaries are extremes, and it is reasonable to study them in terms of the coinciding extremes of environmental conditions. There is the further fact derived from culture work and other laboratory investigations that most organisms have a given range of temperature over which survival is possible, and within the survival limits a somewhat narrower range of conditions over which reproduction and repopulation can be completed. Four critical levels can be recognized in these relationships, and are readily identified with the seasonal boundary conditions as in the following scheme:

Minimum Temperature for Survival—Winter poleward boundary
Minimum Temperature for Repopulation—Summer poleward boundary
Maximum Temperature for Repopulation—Winter equatorward boundary
Maximum Temperature for Survival—Summer equatorward boundary

This scheme summarizes, in effect, the previous comments.

Obviously, for a given species a given boundary point—poleward or equatorward—must depend on only one of the two possibilities. In general the choice will be determined by which of the two critical temperature conditions occurs geographically nearer to the center of dispersal—i.e., the limiting tolerance which would first be exceeded by further spreading of the species. Survival of the individuals and repopulation are both necessary for sustained, permanent establishment. The choice will also be influenced by the actual range of temperatures separating the two possible critical intensities in the physiology of the organisms. Thus, many forms are able to survive temperatures down to freezing, but reproduce only under rather warm conditions. Poleward boundaries of such species are almost certain to be summer ones established by the reproductive requirements. On the other hand, species whose minimum survival tolerance and minimum temperature for reproduction are close to the same intensity are more apt to be limited by liability to winter killing of the adults.

The Four Types of Zonation

On these grounds there appear to be four basic types of zonation which can be recognized, Figure 1. These types are defined in terms of the sorts of boundaries at their poleward and equatorward limits. The simplest type is that in which the extreme temperatures for survival of the individuals are critical both north and south. This involves a winter temperature toward the pole and a summer temperature toward the equator, and is designated as Type 1. Type 2 is the exact converse of Type 1, and covers distributions bounded at both ends by temperatures required for repopulation, i.e. summer temperatures toward the poles and winter temperatures toward the equator. Types 3 and 4 are combination types, one boundary in each case depending on survival tolerances, and the other on reproductive requirements. Both boundaries in Type 3 are related to summer temperatures, and both boundaries in Type 4 to winter conditions.

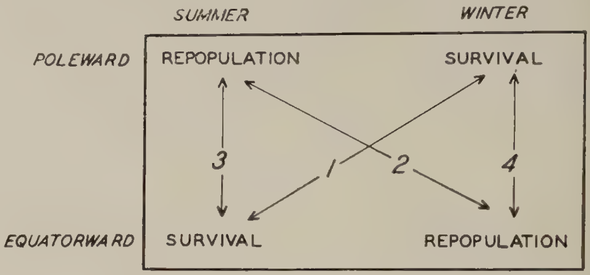

Fig. 1. Diagram of the four basic types of zonation, showing for each the season providing the critical poleward and equatorward conditions. The terms inside the box suggest the most usual sort of relationships involved —i.e. survival tolerance of the most resistant stage, or the requirements for some phase of the process of repopulation.

These four types are, in themselves, adequate for the interpretation of the distributions of many species. There are, however, more complex distribution patterns known whose analyses require inclusion of some further specific details of the life histories. Three such types may be noted briefly as illustrations of the point.

A common type is the seasonally extended distribution. Here, the species occupies a permanent range with at least one boundary of the survival sort. Given a motile stage, larva, or spore capable of dissemination by currents or winds, such a species may spread considerably beyond the survival boundary during the favorable off season, as toward the north in summer. Thus, many tropical forms appear more or less regularly during summer in Woods Hole waters, but are killed back again in the ensuing winters.

A somewhat comparable case may be found with a repopulation boundary involving the actual process of reproduction, as opposed to a larval tolerance. Beyond such a boundary a fringe population can be established which is maintained entirely by new infiltration from the permanent range. Under some circumstances the apparent outer boundary of the fringe area can be quite irrational as regards temperature, since it may be determined chiefly by the distance from the breeding stock over which dissemination is possible. Comparable distributions may result also from vegetative propagation beyond the breeding range, but presumably such processes more often lead to survival boundaries.

A third kind of variant distribution involves alternate mechanisms for the same boundary (poleward or equatorward), reproduction being critical on some coasts and survival on others. This is possible if the two physiological critical intensities are only moderately separated, due to the more extreme combinations of seasonal temperatures on some coasts as compared with others. Such a type of distribution is an inference based on the relationships to temperature accepted as conditioning boundaries. It is extremely interesting, therefore, that seemingly good examples already have come to light. The best of these is for the barnacle *Balanus amphitrite,* which appears to have poleward limits alternately established by inability to survive winter monthly means of about 45° F., and inability to reproduce if summer monthly means do not attain about 65° F. On some coasts one, and on some coasts the other, serves as the limiting factor.

The Importance of Zonal Typology

The importance of recognizing four basic types of zonation becomes apparent in considering the distribution of temperature. As already mentioned, the amplitude of the annual temperature curve varies from place to place. Summer and winter temperatures embrace much wider extremes in temperate latitudes than in the tropics or in polar waters, where relatively more constant temperatures prevail. In temperate latitudes, moreover, more extreme combinations of temperatures are found on the western shores of oceans than on the eastern ones. Along most of the North American Atlantic Coast, the annual range at any point is 25° F. or more, while in European surface waters the range seldom exceeds 15° F. A similar difference holds between the Asiatic and American Pacific coasts. It follows that points on two coasts which have the same temperature at one season may have very different temperatures at the other season. Thus, in the Woods Hole region, the average maximum and minimum monthly mean surface water temperatures are around 68 and 38° F. The equivalent point on the European coast for summer temperature is about at Cape St. Vincent, Southern Portugal. The minimum (winter) monthly mean at Cape St. Vincent, however, is only about 58°, and to match the 38° found at Cape Cod, it is necessary to go well into northern Norway, to a point which in summer has a maximum monthly mean of only 50° F. Cape Cod thus is cotemperate with two points in Europe, one summer and one winter. These points, in turn, are cotemperate with other places on the American coast during the alternate seasons.

Because of such variations in the distribution of temperature, the four types of zonation result in geographically distinctive distributions of organisms. The four types, in fact, cannot lead to congruent patterns of occurrence, as is shown most simply by an example, Figure 2.

In Figure 2, maximum (summer) and minimum (winter) monthly mean temperatures at Newfoundland and at Cape Hatteras have been taken to limit distributions exemplifying the four types of zona-

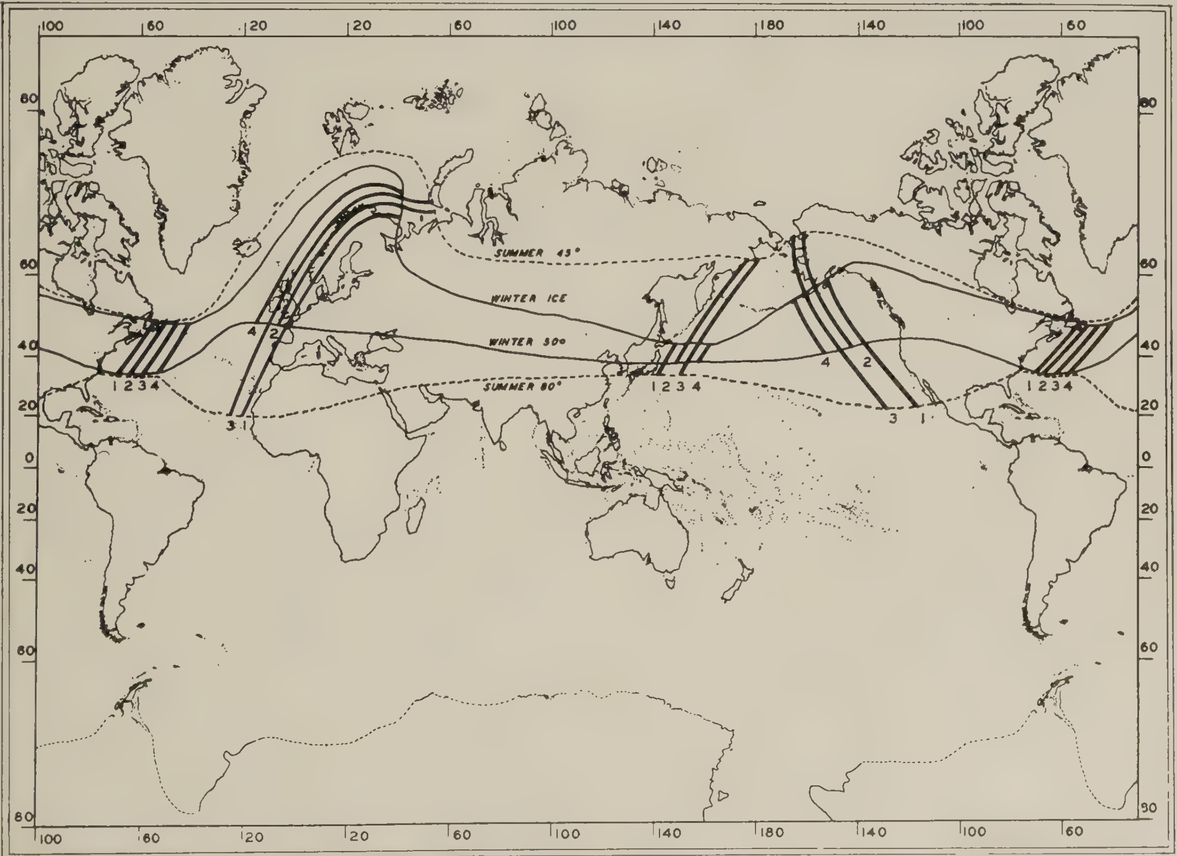

FIG. 2. Diagram showing the geographical extent on the major coasts of zones of the four types, using as limiting intensities monthly mean temperatures of surface water at Newfoundland and Cape Hatteras. The four types of zones are coextensive on the American Atlantic coast, but have independent, distinctive patterns of occurrence on other coasts.

tion. The respective values used are 45° and ice at Newfoundland, and 80° and 50° at Cape Hatteras. On the American Atlantic coast, the four types of zonation are thus given coextensive geographical ranges. The equivalent extent of each of the four types has then been determined for the other major coastlines, using the monthly mean temperature data from the Hydrographic Office "World Atlas of Sea Surface Temperatures" (1944). The isotherms in Figure 2, it may be noted, are schematic, and valid only for the major coastlines.

Since the four critical temperatures occur at separate places on each of the other coasts, there are considerable differences in the configuration of the zones of the four types. Four geographical ranges correspond on every other coast to the Newfoundland-Cape Hatteras range when defined by these temperatures, but no two of the four are coextensive on any other coast. It would thus be possible for four species, one belonging to each type, to have the same range on the American Atlantic coast, but entirely different latitudinal distributions elsewhere around the world.

Distributions conforming to these various sorts of patterns are common. For some species there is also evidence from physiological or other studies supporting interpretation of the distribution in terms of one or another zonal type and with particular limiting intensities. Two may be mentioned briefly, the common barnacle *Balanus balanoides* and the mussel *Mytilus edulis.* They appear to illustrate very closely, respectively, the type 2 and 3 zones of Figure 2, and because of this and certain other facts, the southern boundaries are of greatest interest.

The distribution of *Balanus balanoides* is indicated by some representative records plotted in Figure 3. The southermost limits are at Cape Charles, Virginia (Richards 1930); the English Channel region (Moore & Kitching 1939); Akkeshi Bay (Hiro 1935); and Sitka (Henry 1942). The species seems not to have been reported authentically from Puget Sound, or the southerly Atlantic waters of America and Europe. This group of limits is better approximated by the minimum monthly mean of 45° F., as shown, than by the isotherm for any other monthly mean temperature.

The winter equatorward boundary implies that a low temperature required for repopulation is critical. It is striking, therefore, that while *B. balanoides* larvae settle and attach during the summer toward the north, as in Kola Fjord (Zenkewitsch 1935), fertilization occurs in late fall in the southerly parts of the species' range, as at the Isle of Man (Moore 1935), with attachment taking place in mid- or late

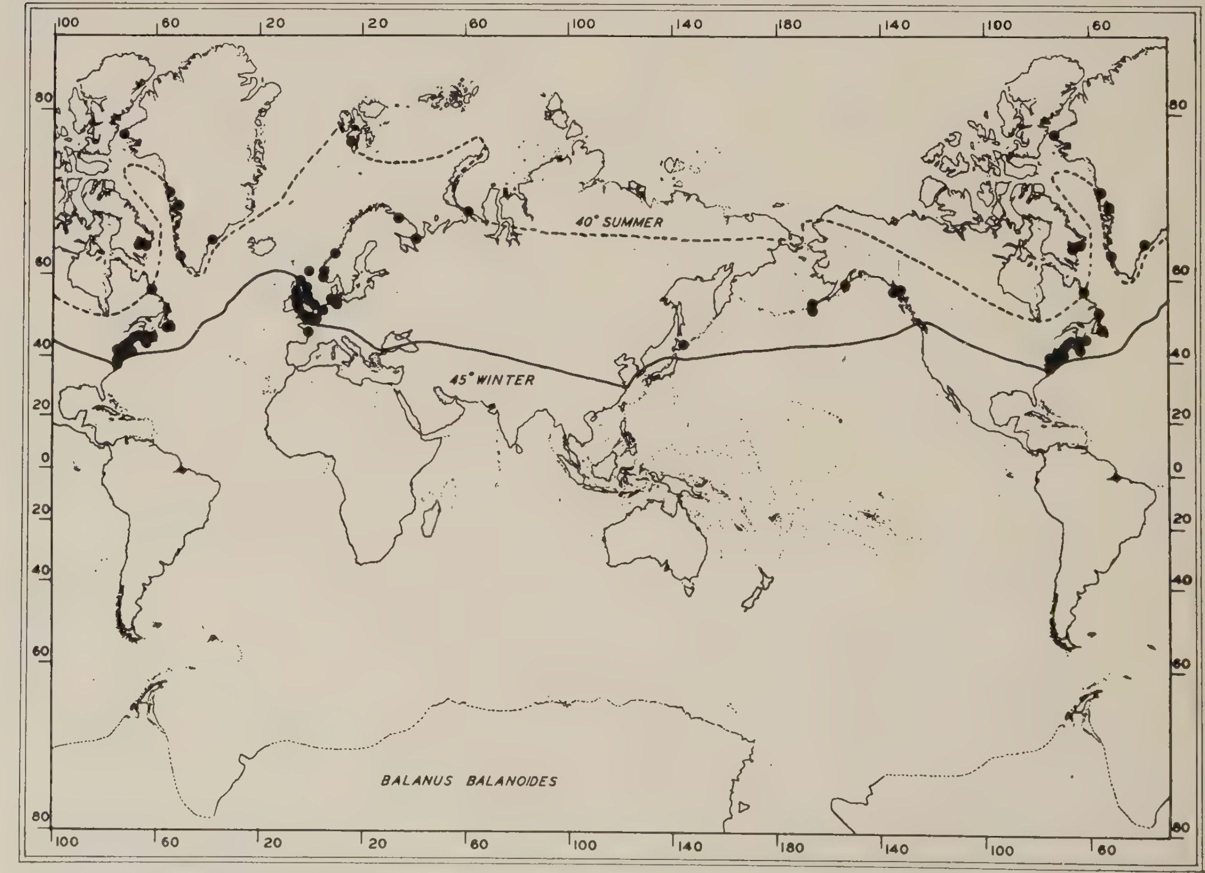

Fig. 3. Some records of the barnacle *Balanus balanoides,* showing particularly the apparent southern limits of the species. These limits are best fitted by the isotherm of the minimum monthly mean (winter) surface water temperature of 45° F.

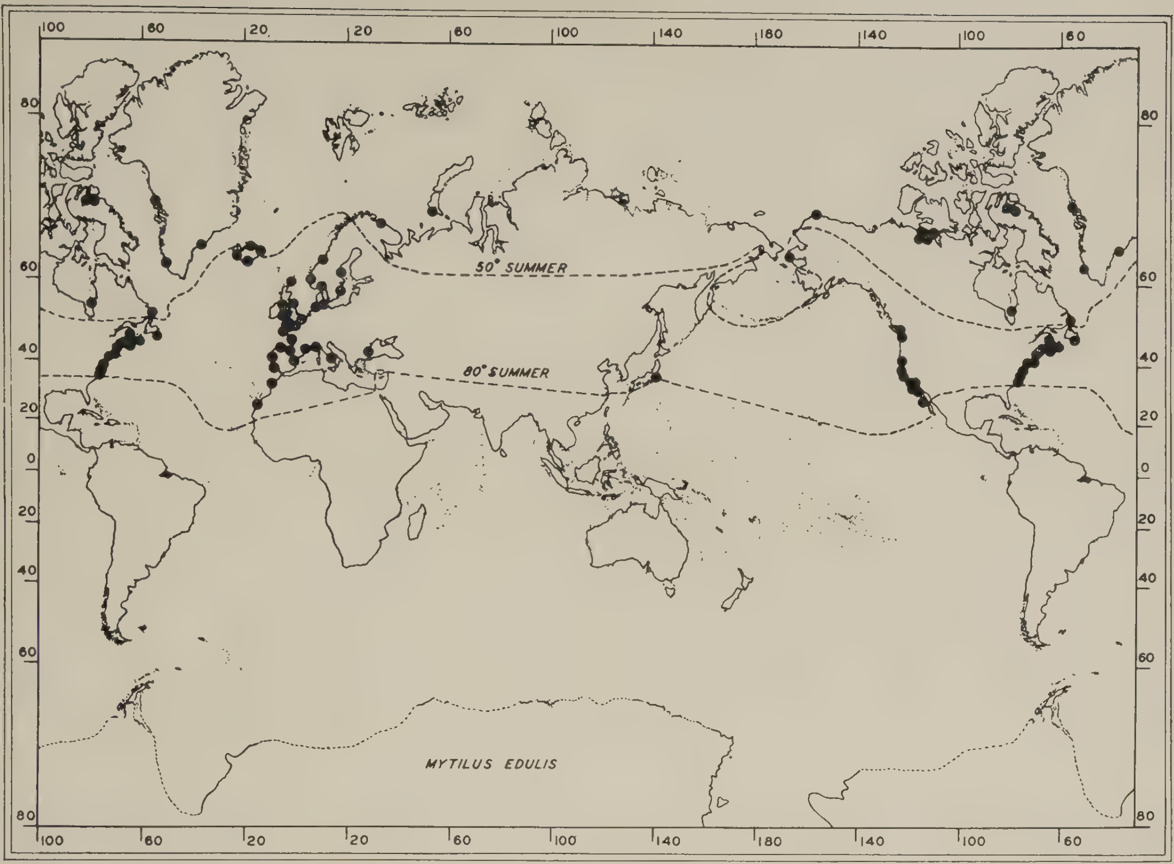

FIG. 4. Distribution of *Mytilus edulis,* with special reference to the southern limits. These are best fitted by the isotherm of the maximum monthly mean (summer) surface water temperature of 80° F.

winter. Winter is also the important season for repopulation on the American Atlantic coast south of Cape Cod. Attachment in Long Island Sound occurs when water temperatures are at or near the minimum, in February or March. Larval stages are present at Woods Hole in the winter (Fish 1925), where attachment occurs in February, March or April. Attachment occurs at intermediate seasons in the middle portions of the species' range, as in June at Lamoine, Maine (Fuller 1946). Utilization of winter conditions to the south for repopulation is therefore clear. The interpretation derives final support from the note by Moore & Kitching (1939) that spawning is not accomplished by adults at the extreme limit of distribution in English waters.

Mytilus edulis (Fig. 4) has a similar extent on the American Atlantic coast, the most southerly records being from Beaufort, North Carolina (McDougall 1943, among others). The form is not common south of Chesapeake Bay.

The limit at Beaufort agrees quite exactly with what is known as to the maximum temperatures at which survival of adults of the species is possible. Ritchie (1927) determined by laboratory experiments that large mussels were killed in water of 84° F. after 14 hours' exposure, though they survived this temperature if transferred to colder water after a 4-hour exposure. Subsequently, it was found that mussels failed to grow in a conduit carrying seawater periodically warmed to 83-90° F., though they grew profusely in a colder section. Bruce (1926) reported complete recovery after 1 hour at 86°, but indicated that longer exposures or slightly higher temperatures would be lethal. In view of these data, it is highly suggestive that even weekly mean water temperatures in Beaufort Harbor are about 83° F., with occasional maximum temperatures of 86-88° (McDougall 1943). Presumably the species is here at its greatest limit of tolerance, and the occurrence of slightly more extreme conditions to the south prevents its further dispersal in that direction.

The mussel's distribution on other coasts is less satisfactory for study, chiefly because the records for a number of varieties and even other species are confused with resultant uncertainties in the data (Lamy 1936). In the eastern Atlantic, however, typical living specimens of the authentic *edulis* have been collected at least as far south as Casablanca (Dr. C. J. Fish, private communication), and *Mytilus edulis* has twice been reported still farther south from Rio de Oro by Font y Saugé (1904). It is debated whether all the northern Mediterranean and Black Sea *edulis* records pertain to *galloprovincialis,* or whether both species occur in those areas as the records nominally indicate.

On the American Pacific coast, Dall (1921) and others have recorded *Mytilus edulis* from Bering Straits to Cedros Island, about half way down the outer side of the peninsula of Lower California. Over most of this range it is said to be common, though in the United States waters it appears to occur more often in bays and harbors than along the exposed outer coast. Some, and possibly all of the southern records, pertain to the recently recognized variety *diegensis* Coe (1946).

In Japanese waters, *Mytilus edulis* has a southern limit near Tokyo (Miyazaki 1938).

The various southern limits—West Africa, Lower California, and Tokyo—are consistent with that at Cape Hatteras, if the latter is interpreted as dependent on the maximum temperature which adults can survive. This is shown in Figure 4 by the course of the isotherm for the extreme summer limit of the monthly mean of 80° F. The southern boundaries of *Mytilus edulis,* in fact, are almost exactly those expected from Figure 2. It is obvious, of course, that the correlation with a monthly mean temperature involves a symbolic use of the latter; in general the 80° F. summer monthly mean is to be taken as indicating the occurrence of various combinations of conditions, partly suggested by preceding discussions, which actually are critical for *Mytilus edulis.*

The northern boundaries of both *Balanus balanoides* and *Mytilus edulis* can not be ascertained from present data. Most of the records plotted are from Madsen (1936) and Dall (1919). The more northerly of these records for both species refer to isolated, relict populations surviving in warm fjords or similar localities, and it is not possible to discover where the general ranges cease and occurrences of this type begin. Such outlying relict populations dependent on local summer warming which exceeds that for the general area, however, are in themselves characteristic of reproductive boundaries. Evidence too involved to present here, but based largely on times of attachment of the two species at a number of localities, suggests tentatively that the critical northern temperature for *Balanus balanoides* might be represented by the 40° monthly mean during the time of maximum temperatures, and that for *Mytilus edulis* by the similar monthly mean of 50°. These isotherms are shown on the maps, but are to be thought of only as probable first approximations of the northern limits of the general ranges of the two forms.

Figure 5 is a second map of the extent of zones of the four types, comparable to Figure 2, but based on temperatures obtaining in the western British Isles and at Cape Blanco in Africa. The limiting monthly mean values used at the north are 62° F. in summer

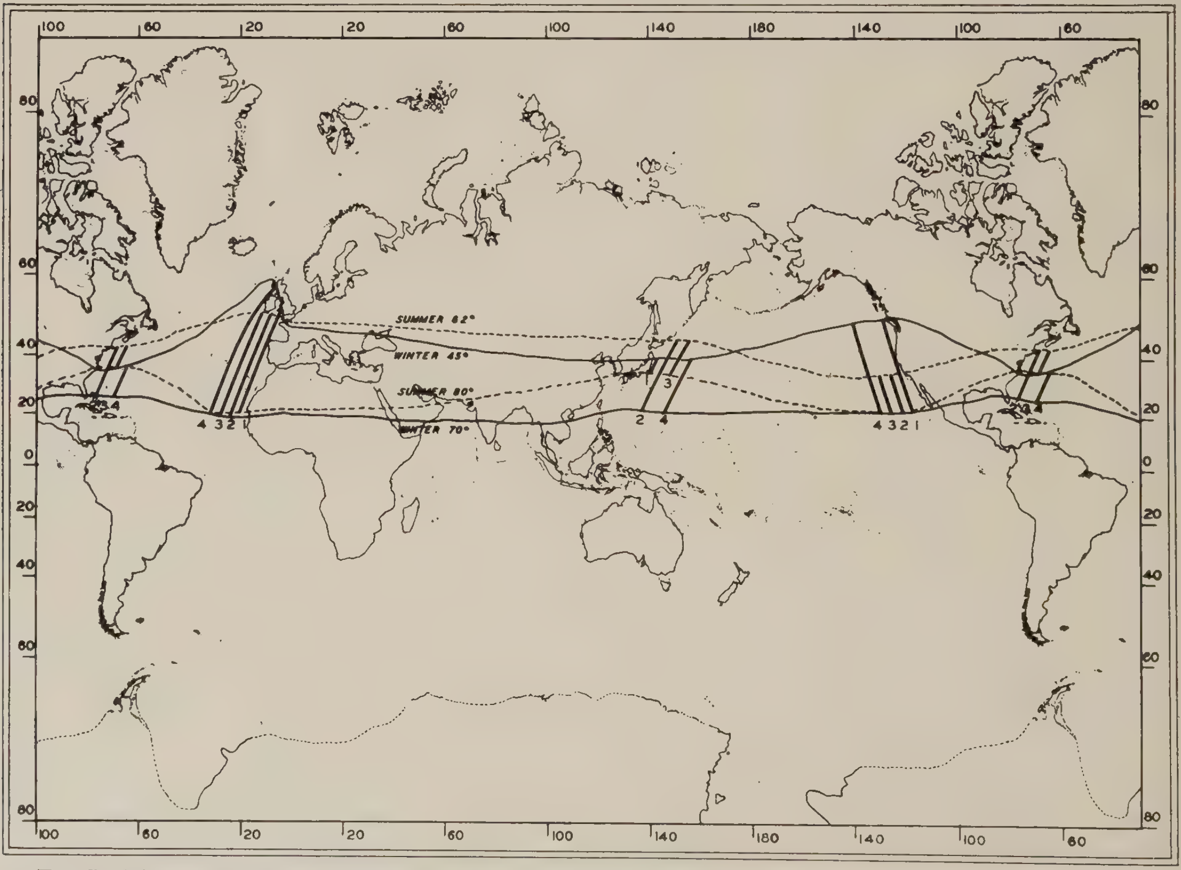

Fig. 5. Diagram of the geographical extent on the major coasts of zones of the four types, using as limiting intensities monthly mean surface water temperatures in the British Isles and West Africa. On the American Atlantic coast Type 1 is excluded, and 3 and 4 are segregated, by occurrence of the northern winter and southern summer limiting temperatures as the same point. Compare with Figure 2.

and 45° F. in winter, and at the south, 80° and 70° respectively. It is again shown that although the four zones are roughly coextensive on one coast, they are not on any of the others. The differences, however, are more extreme, due to the fact that the limiting northern winter temperature and the southern summer one occur at nearly the same point on the American Atlantic coast. As a result, the types 3 and 4, which are of parallel extent in Europe, are entirely separated in American Atlantic waters, and the type 1 zone, with these or narrower limits as regards actual critical intensities, can not occur at all. In Japanese waters the situation is comparable, though not quite as extreme as on the American Atlantic coast.

The Type 1 situation in this illustration is obviously a restatement of the familiar principle that the most steno-thermal European forms are excluded from the American Atlantic coast, owing to the great extremes of temperature obtaining throughout the waters of the latter. A species whose greatest survival tolerances embrace a range of not more than 25° F. can find no place to exist. Zonal typology, however, affords one possible explanation of the fact that only some species are so effected, out of a large number which might appear equivalent from their European distributions. Forms common to the European and American Pacific coasts, but undetected by extensive studies on the American Atlantic coast, are especially open to interpretation as very steno-thermal Type 1 species. The case of the hydroid *Syncoryne eximia,* shown in Figure 6, is an example. For these records I am obliged to Dr. E. S. Deevey, Jr.

INDEPENDENCE OF NORTH-SOUTH SYSTEMS OF ZONES OF THE FOUR TYPES

It appears, then, that four basic types of zonation need to be considered in studies of distribution. Each of these types must lead to the development of a complete system of zones over the world, utilizing the entire available temperature gradient with various combinations of limiting intensities. An indication of the implications of this conclusion can be obtained from a brief, simplified consideration of the American Atlantic coast.

On the Atlantic coast, important well-known biotic changes occur in the vicinity of Newfoundland, Cape Cod, Cape Hatteras, and along the Florida coast. Palm Beach may be taken here as the focal point for the latter. Using just these four change-points, fifteen components can be recognized in the whole biota from the Arctic to the Tropics, Figure 7. Fourteen have at least one termination along the coast—i.e., they are zonal—while the fifteenth is ubiquitous. This is the conventional, generalized picture arrived

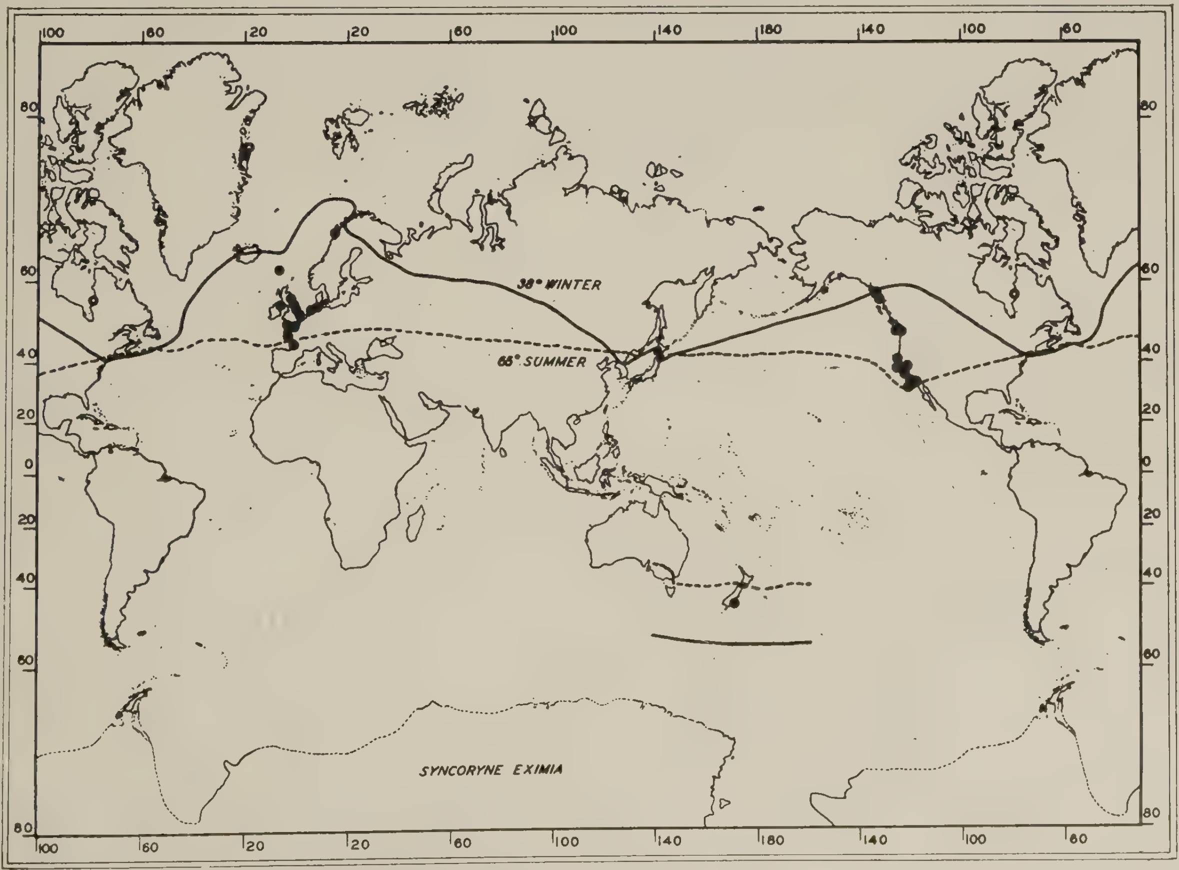

FIG. 6. Distribution records of the hydroid *Syncoryne eximia.* The main body of data agree with a Type 1 zonation as in Figure 5, with the limiting intensities indicated.

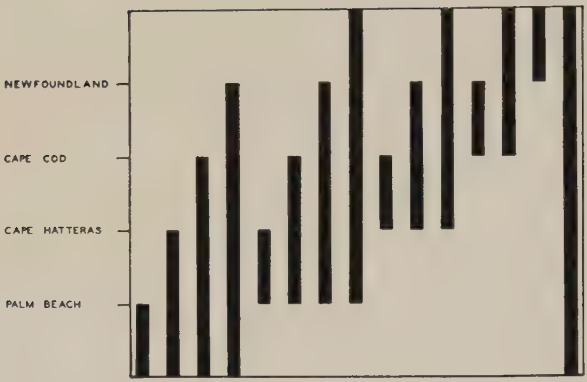

Fig. 7. Schematic representation of the components of the American Atlantic coast biota, with reference to the important change-points of Newfoundland, Cape Cod, Cape Hatteras, and Palm Beach. Fifteen possible ranges exist, of which fourteen are zonal and one is ubiquitous.

at by considering only the geographical ranges and describing them in terms of the four boundary localities.

The temperature data of the Hydrographic Office (1944), Parr (1933), and Fuglister (1947), show that at the times of maximum and minimum conditions, the isotherms are largely bunched at these same change-points, which thus are the locations of the temperature breaks (marked changes occurring in a short distance) with which biotic distributional data are correlated. On a scale of generalization comparable to that in the biological data above, these temperature breaks can be thought of as including all of the isotherms of the entire gradient occurring between Newfoundland and Florida. Neither generalization, of course, is strictly true, but they serve satisfactorily for present purposes.

The temperature breaks do not occur in both seasons at all the localities. At Cape Cod there is no break during the time of minimum (winter) temperatures, and in the Palm Beach area there is little or no thermal differentiation during summer. Newfoundland and Cape Hatteras, however, have breaks involving both maximum and minimum conditions. It may be assumed that at localities having a break at only one season, all the distributions terminating there are to be correlated with that break. If breaks occur in both seasons, then some of the distributional boundaries presumably are related to one season, and some to the other. It will further be assumed, here, that the sharpness of a biotic break is a direct reflection of the severity of the temperature break—i.e., the number of species affected in a given instance depends on the number of degrees of temperature change.

On this basis a provisional analysis of the Atlantic coast biota can be made in terms of zonal typology, showing the possible mechanisms underlying the geographical ranges of Figure 7. This has been done in Figure 8. Between Cape Cod and Palm Beach, each of which has a temperature break in only one season, only one type of zonation can exist (Type 2, limited by summer conditions to the north and winter to the south). For ranges bounded by either of these points and by a locality having breaks in two seasons, two zonal types are possible. Between Cape Hatteras and Newfoundland, each with breaks in both seasons, all four zonal types may be found.

In Figure 8, ranges which extend into the Arctic and Tropics have been handled as follows. Water of essentially uniform coldness is found in the Arctic

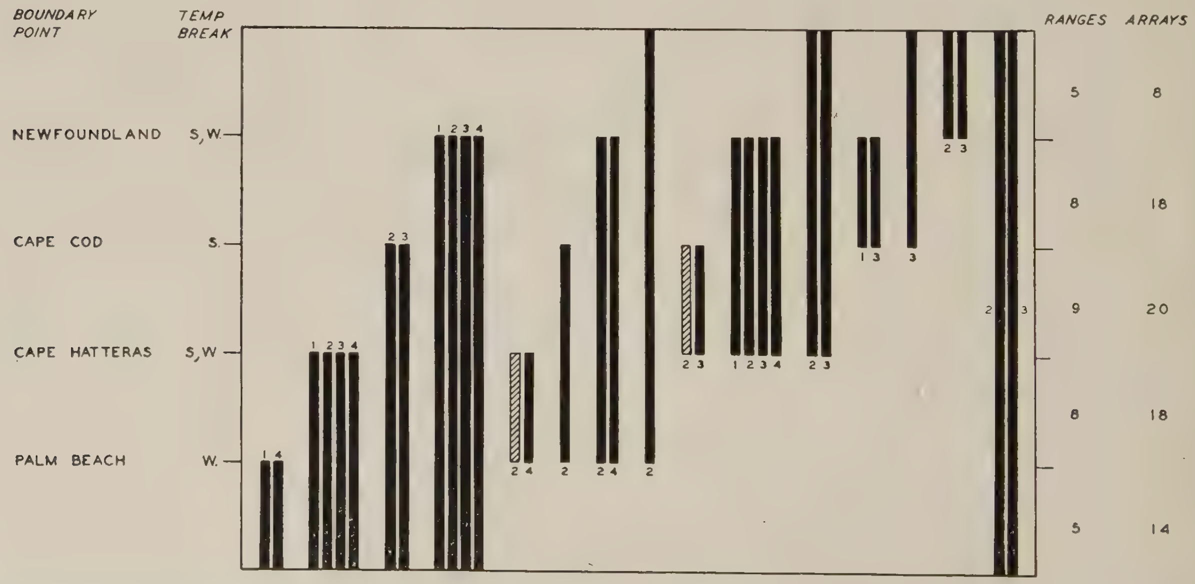

Fig. 8. Analysis of the biotic components in Figure 7 by zonal types. The summer and winter temperature breaks at the four change-points are indicated by initials. A separate bar (array) has been drawn for each zonal type contributing to each geographical range. The small figures show the type of each array. The figures at the right show the number of ranges and arrays contributing species to each province between breaks. For further explanation see text.

under the winter ice, and it is therefore taken as improbable that any poleward boundary north of the winter ice line (Newfoundland) is referrable to winter conditions. Summer alone is critical in the Arctic. This view, of course, is valid only for aquatic species. As for forms extending through the tropics, these exhibit no equatorward boundary, the southern hemisphere limit being a mirror image of that in the north. For theoretical treatments it must be assumed that some of these species have potential equatorward boundaries related to each season. In other words, if the entire annual temperature curve in the tropics were raised until the tropics became completely uninhabitable, some of the equatorward boundaries that would eventuate in the process would be conditioned by the new winter temperatures, and some by the new summer ones. This is the general analytical procedure that must be applied initially to any group of distributions extending *through* a center of warmth or coldness. Similar reasoning, it may be noted, has to be used in dealing with endemic species in places like the Gulf of Mexico or the Indian Ocean, where northern limits can be determined by geography rather than temperature, and true zonal boundaries may not be available for study.

The major general principle demonstrated by Figure 8 is that no zonal type contributes, at least in any significant measure, to all geographical ranges. By the way in which seasonal temperatures are distributed, each type is restricted to a definite pattern of possible north-south combinations based on actual intensities, and the pattern of possibilities is forced to be distinctive for each of the four types. The generalizations involved in grouping both the biological and temperature data for Figures 7 and 8 would allow, actually, for a few additional ranges and arrays—as a zonal type for a given range may be called—but these presumably would be exceptional cases without statistically important effects on the over-all conclusion.

At the right of Figure 8 the numbers of ranges and arrays contributing species to each biotic province are tabulated from the data in the figure. A province is taken as being bounded by any two consecutive boundary points, with a province also for the Arctic and one for the Tropics. The total number of ranges is 15, as noted in connection with Figure 7. Figure 8 shows 33 arrays altogether. It is interesting to note that the picture of distribution in terms of zonal types is very roughly about twice as complex as that in terms of ranges alone.

A point of passing interest is indicated in Figure 8 by the two Type 2 arrays with lined shading. Temperature conditions along the coast are such that in each of these arrays, a single monthly mean intensity is critical at both ends. The same temperature occurs at the northern end in summer that establishes the southern limit in winter. This implies that repopulation could not be carried out either above or below the single intensity, a situation which is obviously improbable as a proposal for any very large number of sessile marine forms. In effect, however, the situation is realized by migratory fish which follow an optimum temperature as it moves back and forth along the coast. Parr (1933) discusses the problem as it applies to the Cape Cod-Cape Hatteras stretch. This is another instance of the great variety of physiological relationships which can lead to a Type 2 zonation.

PROBLEMS OF COMPARING SEVERAL COASTS

The treatment of the Atlantic coast in Figures 7 and 8 is dependent on the existence of well marked breaks in the distribution both of the biota and temperatures, separating regions of relative homogeneity. The contrasts between the breaks and the homogeneous areas are sufficiently strong to lend value to the generalizations as approximate statements of the over-all picture. Similar treatments are possible for some other coastlines. There are coasts, however, which are much less easily divided into a few reasonably well defined provinces. Both the biotas and temperatures along such coasts change gradually, or at best have more numerous, comparatively small breaks none of which involve large numbers of species or isotherms. The European coast tends to be of the latter character, judging from the discussions by Ortmann (1896), Ekman (1935) and others. Ekman thus is notably careful to point out that an element of convenience, at least as much as any obvious natural facts, underlies his proposed boundary at the English Channel, separating his boreal North Sea region from the littoral of Southern Europe.

In dealing with coasts like the European, many more geographical ranges and arrays of distribution have to be recognized in order to attain a degree of truth comparable to that for the American coast in previous discussions. Since essentially the same total gradient of temperatures from maximum tropical heat to permanent polar ice is available on both sides of the Atlantic, for example, it follows that a number of arrays of one zonal type in European waters must be equivalent to a single array on the American side. The winter break in Florida includes monthly mean temperatures from about 55° to nearly 75° F.; in the eastern Atlantic, these same minimum winter temperatures are distributed from northern Spain to somewhat south of Dakar. Species common to the two coasts and bounded by such temperatures can differ considerably in European-African distributions, depending on their individual critical intensities within this 20° range, though all will share roughly the same boundary point on the American coast. Even in biogeographic comparisons of coasts with equally well marked breaks, similar difficulties must arise unless the temperature breaks on both comprise identical intensities, which is seldom the case for even one pair of breaks.

It is evident from such considerations that no very satisfactory map or other representation can be developed showing zonal distributions throughout the world at large. Each coast is sufficiently unique so that generalized intercomparisons have to sacrifice practically all fidelity to detail, vitiating their interest and usefulness.

Although somewhat more bluntly stated, this conclusion does not differ in tenor from those reached or implied by many previous workers. Zonal typology, by showing how intricate the possibilities are for the merging, separation, and recombinations of distributions of organisms, provides a general formal basis for appreciating the truth of such views.

It is of interest in this connection to note how closely zonal typology has been approached by marine biogeography. Most investigators agree in recognition of a strong, well defined tropical zone. Commonly the boundaries of this are established where winter temperatures first drop significantly and conditions of relatively constant warmth no longer prevail. Ortmann (1896) used almost these words, for instance. In the high arctic, likewise, emphasis has been placed on seasonal conditions in interpreting the occurrences of organisms. The first departures from relatively uniform coldness throughout the year are caused by summer warm-ups of surface water, the importance of which is shown among other ways by the limitation of some arctic forms to cold, deep waters in southerly parts of their ranges. It seems to be only the failure to carry these principles of seasonal boundaries to logical conclusions respecting the temperate zones that has prevented an earlier statement of the thesis of the present contribution. It is remarkable that study of the American Atlantic coast did not lead to such conclusions long ago; the summer Cape Cod temperature break and the winter Florida one, each of which coincides with poleward and equatorward boundaries for many species, together predicate the whole argument.

The most extraordinary conclusions in this respect were reached by Setchell (1915 *et seq.*), whose ideas were very similar to ones still current in much terrestrial work. Setchell proposed to recognize a series of zones bounded by summer temperatures. These zones he then demarcated into subzones on the basis of the winter temperatures within them. Clearly this view incorporates all the fundamentals necessary to the present suggestion of multiple types of zones defined by their seasonal boundary relationships.

The difference of Setchell's conclusion from the hypothesis of multiple zonal types appears to have been conditioned by a preconception common in biogeography, namely that the world should be divisible into *one* series of geographically contiguous belts that will represent the main features of biological distribution. Probably this is a direct heritage from the historical background of regional faunistics and floristics, reinforced by the natural inclinations of the mapmaker and descriptive geographer. Granted a predisposition of this sort, proposals such as Setchell's are unavoidable consequents. It is inconsistent, however, to expect a single system of zonation to summarize even the empirical diversity of biological distributions, and certainly such a system is inappropriate as an interpretive summary for distributions differing in kind because of distinctive causes of limitation. Since both maximum and minimum temperature conditions need to be considered, and since there is no rigid parallelism in the occurrence of the two, temperature itself can not be treated in biogeographical analysis as if it had but one variable, and a single series of temperature-controlled zones is impossible. It need hardly be added that any attempt to circumvent this fact by use of annual mean temperatures or similar methods is invalid.

APPLICATIONS OF ZONAL TYPOLOGY

The analysis of distribution by zonal types lends itself to a number of applications. First, it may be noted that the procedure is applicable to other conditions than temperature. Any seasonally variable conditions of comparable biological importance can be dealt with in the same way. As one example, the distribution of organisms in estuaries as related to salinity undoubtedly involves various types of salinity zones analagous to those related to temperature.

So far as temperature is concerned, study of distributions in terms of zonal types can be of use in guiding transplant work with commercially valuable forms, in predicting biotas of unexplored regions, and in various similar ways.

The most interesting possibility, however, concerns the determination of prehistoric environmental conditions. By studying the fossil distributions of selected series of forms, it should be possible to map the distribution of maximum and minimum monthly mean temperatures for earlier oceans. From these, in turn, some approximation of annual temperature curves might be inferred, opening up many avenues of inquiry for a science of paleo-oceanography. Merely as one example, Dr. Hutchinson in his contribution to this symposium has discussed the belief that the arctic has been appreciably warmer in the past than at present. It would be of great interest to know whether that warming involved significant differences in both summer and winter temperatures, or whether the summers only were affected. In the latter case there have always been low tmperatures at least in winter, which might greatly simplify the problem of the evolution of the present arctic fauna by justifying the existence of ancestral stocks suitably adapted to cold. There are independent reasons, of course, for an assumption that summer temperatures were chiefly affected, but a study of the fossil record conceivably could provide factual evidence with data on the the actual intensities.

SUMMARY

The main points of this contribution can be summarized in three sets of conclusions:

1. Zonal boundaries of organisms are to be interpreted in terms of summer and winter temperatures.
2. Four basic types of zonation can be recognized, each having a distinctive combination of summer or winter boundaries for its poleward and equatorward limits.

3. Zones of the four types have distinctive configurations around the world, and independent patterns of north-south occurrence. These facts depend on differences in distribution of summer and winter temperatures.

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Contribution No. 375

OXYGEN CONSUMPTION IN SEA WATER OVER LONG PERIODS[1]

By

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The rate and extent of oxygen consumption in sea water have been studied and measured under a variety of conditions and for a variety of purposes. Such studies, of what is often called the "biological oxygen demand," have either been involved in the estimation of the total content of organic matter or have contributed to the understanding of the processes of organic decomposition in the sea. They have usually consisted of bottling samples of the water and storing them for varying periods, generally at controlled temperatures, determining the oxygen content of the samples and comparing it with the content of the original water. The incubation time has seldom exceeded a few days, or at most a few weeks.

It has generally been supposed that oxygen consumption will continue, perhaps indefinitely, at a diminishing rate. But no one has apparently determined how long it will take for the process to become entirely imperceptible.

As would be expected, the rate and extent of oxygen consumption depend upon the temperature, the time of storage, and the source of the water, which determines the amount and character of the organic matter present.

Oxygen consumption is one of the factors concerned in the distribution of oxygen in the sea, and especially the occurrence and significance of the "oxygen minimum." Sverdrup (1938) has shown the mathematical consequences of the various possible assumptions concerning the rate of oxygen consumption and the distribution of oxidizable organic matter. Seiwell (1937) determined the oxygen consumption in sea water samples from various depths, incubated for ten days at two temperatures, 11° and 25° C. Extrapolating the time, he calculated the annual consumption at temperatures *in situ*. His results were many times in excess of values which he had calculated from the

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study of the oxygen distribution in the sea, and his conclusion was that in the ocean there are restrictive influences which limit oxygen consumption.

While it is to be expected that experimental laboratory conditions will yield results very different from those in the ocean, it seems that the closest approximation to the natural process would be to take sea water samples from various depths and to incubate them for as long a time as possible at the temperature which the water had *in situ*, removing samples for analysis periodically.

Water was obtained from two stations, "B" and "C," located respectively at 39° 05′ N., 70° 40′ W. and at 35° 30′ N., 67° 30′ W. The most significant part of the water column is the oxygen minimum layer. Samples were accordingly taken from this level (230–250 m. at Station B and 900–920 m. at Station C), as well as from the surface and from a depth well below the minimum (1240 m. at Station B and 1725 m. at Station C). The "minimum" samples were immediately placed in glass-stoppered bottles of about 250 ml. capacity and incubated in a water bath in the dark at 8° to 9° C., their original temperature. The deep samples were similarly stored at a temperature of 4° to 5° C. The surface samples were distributed, some of them at 8°, some at 4°, and some at the uncontrolled laboratory temperature, about 25° C. Bottles were removed for analysis periodically over a period of nearly two years (713 days).

All analyses were made in duplicate (from a single bottle in storage) by the routine Winkler method. A single solution of sodium thiosulfate was used for the whole period and its concentration determined before each analysis by titration against standard KIO_3 and $K_2Cr_2O_7$. Several standards were prepared during the experiment and cross-checked against each other.

Due to misunderstanding, different solutions were used in the original determinations of oxygen content, made on shipboard, so that the first two analyses for each sample were considered unreliable and are not included in the results given. However, since the object of the experiment was to follow the long-term changes, rather than those which took place in the first few days, this is not considered a serious gap in the data.

The results are shown in Table I. It will be seen that the surface samples, from both stations, were erratic, especially those incubated at 25°. The surface samples incubated at each of the lower temperatures were more regular and came to a constant level (depending on the temperature) after about 100 days of incubation. Significantly greater consumption resulted at the higher temperature, even after two years.

TABLE I. CONSUMPTION OF OXYGEN (O_2 ml./L) IN WATER FROM THREE DIFFERENT LEVELS AT TWO STATIONS. WATER WAS STORED IN THE DARK AT TEMPERATURES (C.) CLOSE TO THOSE *in situ*, IN SMALL INDIVIDUAL BOTTLES, ONE OF WHICH WAS USED FOR EACH ANALYSIS. TIME IS MEASURED FROM THE DAY THE WATER WAS SAMPLED

Time (days)	*Station B*					*Station C*				
	Surface			*"Minimum" (230–250 m.)*	*Deep (1240 m.)*	*Surface*			*"Minimum" (900–920 m.)*	*Deep (1725 m.)*
	25°	*8–9°*	*4–5°*	*8–9°*	*4–5°*	*25°*	*8–9°*	*4–5°*	*8–9°*	*4–5°*
18	4.11	4.50	4.68	3.55	6.38	3.62	4.05	4.15	3.54	6.18
42	4.18	4.28	4.15	3.50*	6.13	1.49	3.40	4.10	3.43*	6.07
66	3.83	4.16	4.08	3.34	6.06	3.25	3.92	3.95	3.43	5.99
85	3.93	4.22	3.96	3.26	6.02	1.21	3.44	3.79	3.43	5.98
113	3.85	3.78	3.85	3.27	6.14	3.09	3.76	3.77	3.40	5.95
148	—	—	—	3.31	6.12	—	—	—	3.43	6.04
200	—	4.06	—	3.21	6.13	—	3.43	—	3.41	5.98
260	3.51	—	3.76	3.32	6.23	2.60	3.06	—	3.44	5.97
323	—	—	—	3.48	6.05	—	—	—	3.40	6.06
412	—	3.99	3.75	3.47	6.12	—	3.15	3.80	3.42	6.03
583	—	4.11	3.66	—	6.14	1.74	3.14	—	3.44	6.02
713	—	4.15	3.53	3.46	6.11	2.89	—	3.77	3.39	6.01

* At this point samples of this water were raised to room temperature (25° C.); results are shown in Table II.

The most striking fact observed is that within the limits of the analyses there is no net oxygen consumption in either the "minimum" or the "deep" samples after the first 50 days. They remained without change for nearly two years at their temperatures *in situ*. The deep samples were particularly regular in behavior.

The apparent rise in oxygen content in the minimum samples from Station B, after the initial drop, is very likely the result of the conditions of the experiment, and the abnormally large oxygen consumption in some of the surface samples incubated at 25° is presumably due to the accidental inclusion of plankton material or other easily oxidizable substances.

In order to determine the relative importance of the temperature, some of the "minimum" samples were removed after 42 days and incubated thereafter at 25°. The results, shown in Table II, indicate consistently greater oxygen consumption in these samples.

A second series of experiments was begun, primarily to study the

TABLE II. CONSUMPTION OF OXYGEN (O_2 ml./L) AT ROOM TEMPERATURE (25° C.) IN WATER FROM THE OXYGEN MINIMUM LAYER AT TWO STATIONS. WATER HAD PREVIOUSLY STOOD FOR 42 DAYS AT 8–9° C. (SEE NOTE TO TABLE I)

Time (days)	*Station B*	*Station C*
0	3.50	3.43
6	3.34	3.34
20	3.27	3.33
39	3.13	3.40
69	3.10	—
212	2.96	3.27

TABLE III. CONSUMPTION OF OXYGEN (O_2 ml./L) IN WATER SAMPLED AND STORED UNDER CONDITIONS SIMILAR TO THOSE IN TABLE I. TIME MEASURED FROM THE DAY THE WATER WAS SAMPLED

Time (days)	*Surface*	*"Minimum" (400 m.)*	*Deep (1200 m.)*
	25°	*8–9°*	*4–5°*
0	5.11	3.89	6.28
2	5.11	3.84	6.21
20	4.97	3.76	6.17
40	4.80	3.75	—
82	4.41	3.76	6.13
172	4.65	3.81	6.10
305	4.50	—	6.14

consumption in the first few days. Samples were taken from three levels, as before: surface, 400 m. (the oxygen minimum level), and 1200 m. They were incubated at the same temperatures as in the first series (which were the temperatures *in situ*). The results are shown in Table III. The surface samples again behaved erratically, with oxygen consumption continuing for about 80 days. In each of the other sets of samples, oxygen consumption ceased after the first few days.

These experiments do not, of course, give us a clear picture of the process of oxygen consumption *in situ*. One wonders whether the true, natural rate of consumption is the maximum rate noted in the first few days of laboratory incubation or the minimum rate integrated over the whole period. The former assumption leads to the anomaly obtained by Seiwell and already referred to—more oxygen apparently consumed than can conceivably be available. Rather than to attempt to reconcile the situation by assuming *retarding* agencies in the sea, it is more in keeping with known facts to assume that the laboratory conditions *hasten* the normal rate of consumption. Zobell and Anderson (1936), and others, have found bacterial action to be stimulated in bottled samples, because of surface effects. It is impossible to tell to what extent the observed initial rate of consumption is due to such surface concentration of bacteria, but it is probably not entirely due to this.

One also wonders why oxygen consumption ceases after a comparatively short period. It is evidently not the result of complete decomposition of organic matter. Among others, Waksman and Carey (1935) have pointed out that bacteria do not attack and oxidize all the organic matter in the water. Further, they discuss the "dynamic equilibrium" in sea water, involving the organic matter and its decomposition products, the oxygen tension, the temperature, the bacterial population, etc. The unknown condition of the equilibrium must be responsible for the fact that in water which has come to a steady state at low temperature additional oxygen is consumed when the temperature is raised.

It may be significant to observe that the surface samples which were incubated at the lower temperatures eventually reached a level of oxygen concentration similar to that in the "minimum" samples. This lends some support to the view that the organic matter in a vertical water column (at least down to the oxygen minimum layer) is principally derived from the local surface.

Until we know more about the nature and distribution of the dissolved organic matter in the sea, we cannot safely translate such laboratory experiments as these into natural processes. Nevertheless, there is reason to suspect that the natural process of oxygen consumption in the sea is slower than we may previously have assumed.

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Contribution No. 377

THE BIOCHEMICAL RELATIONS BETWEEN MARINE ORGANISMS AND THEIR ENVIRONMENT

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The chemical nature of an aquatic environment is changed by the growth and activity of the organisms which it supports. Photosynthesis by green plants removes carbon dioxide and essential plant nutrients from the water and adds oxygen and organic matter in the form of new living tissue. Decomposition, whether it results from bacterial action, or the respiration of plants and animals, removes organic matter and oxygen and replaces or regenerates the carbon dioxide and essential plant nutrients. These changes may proceed to such an extent that the lack of an essential element may ultimately limit the growth of the very organism which caused the deficiency. Before this extreme condition is reached, however, the changes in the environment may have a direct effect on the composition or physiological state of the organisms. Superimposed on these biological changes are the effects of the motion of the water itself which may transport new supplies of these materials into the area.

Three processes, therefore, must be considered simultaneously in order to secure a complete picture of the changes in the biologically active constituents of the water. These are the assimilation, due to photosynthesis, the regeneration, due to processes of decomposition, and transport, due to the motion of the water.

In the sea most of the elements essential for photosynthesis and plant growth are present in great excess. Available phosphorus and nitrogen compounds, however, are found in only small concentrations, and may be completely removed from the water by the activity of the plants which make up the phytoplankton population.

The assimilation of phosphate and nitrate from the water occurs at different rates, but their concentration in the water is such that they become exhausted at about the same time as a result of extensive phytoplankton growth. If the replenishment of these elements were negligible, plant growth in the surface waters would be at a standstill during a large part of the year. It is the rate of replenishment, and not the concentration observed at a given time, which determines the fertility of an aquatic environment. This replenishment is provided by the two processes of decomposition and water circulation.

The net result of the three processes is to maintain the ratio of phosphorus to nitrogen at a nearly constant value in the sea. Examples of the uniform ratio of these elements in the Atlantic, Indian and Pacific Oceans are given in Figure 1, which is reproduced from a paper by Redfield (1934). Though the concentration of nitrogen varies about 600 fold and that of phosphorus about 150 fold the ratio of their concentrations in the water is never far from 15 atoms of nitrogen to 1 of phosphorus.[2] A similar correlation will be found in this same paper between the changes in the carbonate and the nitrogen content of the water. The constancy of these ratios imply that the organic matter synthesized and decomposed in the sea will contain, on the average, about 16.7 grams of nitrogen and 2.5 grams of phosphorus for every hundred grams of carbon*. These ratios have proved useful, since it is often possible to compute, from observations of one biologically active element, the probable changes in others.

It is pertinent to inquire whether the constancy of these ratios in the sea is determined by the physiological properties of the organisms, and whether living matter produced under different nutritive conditions is uniform in composition.

Experiments on the assimilation of nitrate and phosphate during photosynthesis by the marine diatom, *Nitzschia closterium,* have shown that the rate of assimilation of phosphorus is related to the concentration of both phosphate and nitrate in the medium. The rate of assimilation of nitrate, however, is independent of the phosphate concentration and related only to the concentration of nitrate in the culture medium (Ketchum 1939a). In Figure 2 a grid is presented in which the phosphate concentration of the culture medium is plotted against the nitrate-nitrogen content. Any simultaneous change of these two nutrients is indicated by a line connecting the initial and final concentrations. If the rate of removal of phosphate is relatively great the slope of this line will be steep. If the rate of removal of nitrate is relatively high the slope will be more nearly flat. The lighter lines show the changes which may be expected in the media as predicted from observed rates of assimilation of nitrate and phosphate by pure cultures of *Nitzschia closterium.* The heavier lines show actual simultaneous changes observed in individual cultures of this diatom.

If the physiological activity of this diatom is typical of the action of the phytoplankton population a prediction of the effect of their activity on the com-

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[1] Contribution No. 377.

[2] These ratios have been corrected for the salt error of the phospate analysis as determined by Cooper (1938).

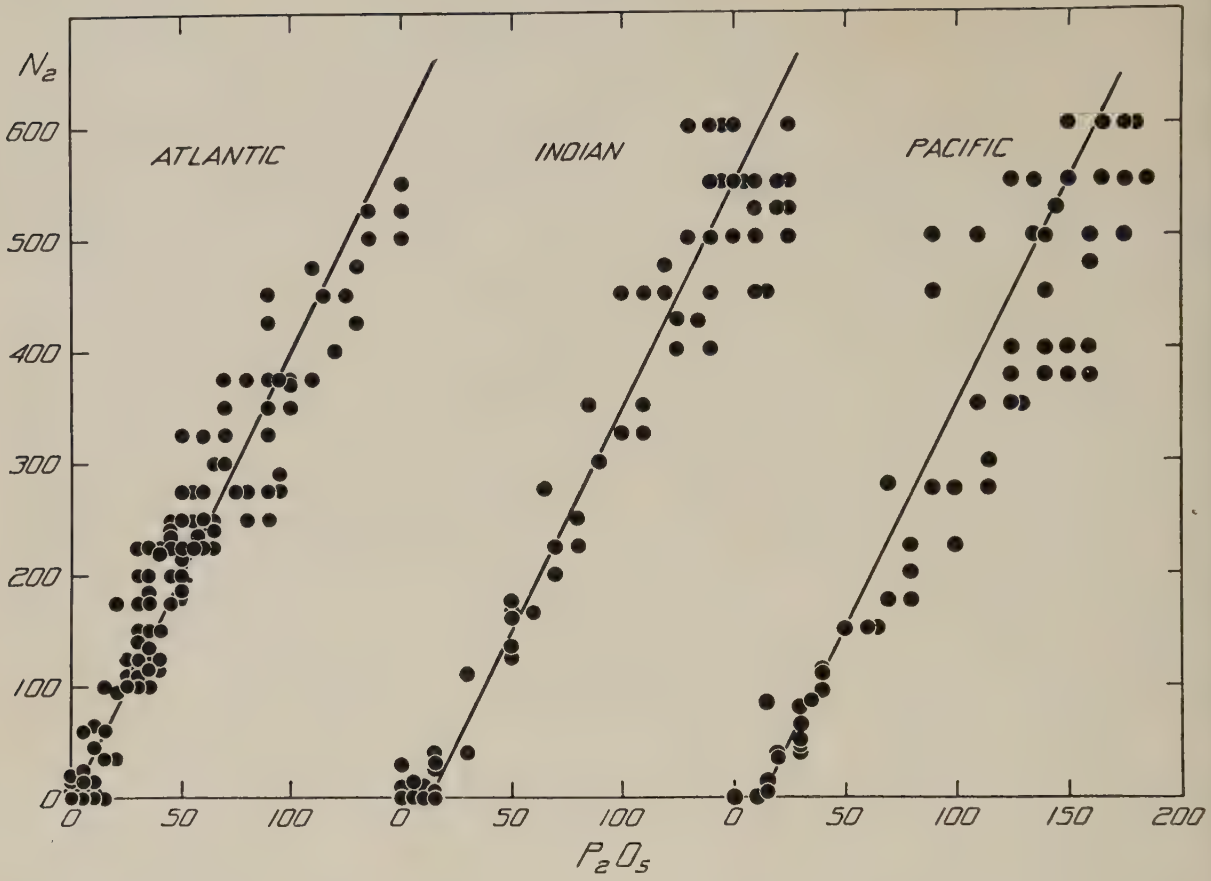

FIG. 1. Correlation between concentration of nitrate and phosphate in the waters of the Atlantic, Indian and Pacific Oceans. After Redfield, 1934.

position of the water may be made. The normal ratio of nitrogen to phosphorus in the sea would be represented in this figure by a line joining zero and the point described by a phosphate concentration of 100 and a nitrate-nitrogen concentration of 220. If the phosphorus:nitrogen ratio in the medium is high the metabolism of the cells tends to change the ratio of the concentration in the water so that it approaches more closely the normal ratio. If, however, the ratio of concentration is low, due to a relative lack of phosphorus, the metabolism of the cells tends to increase the discrepancy.

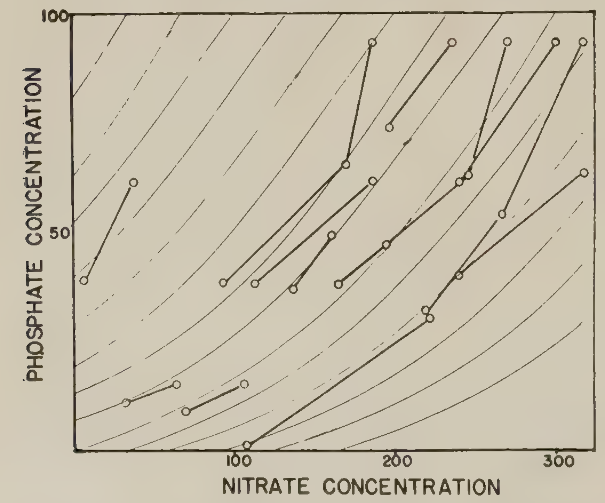

FIG. 2. The simultaneous removal of phosphate and nitrate from sea water of various compositions by the marine diatom *Nitzschia closterium*. Ordinate, gamma N per liter, abscissa gamma PO_4 per liter. After Ketchum, 1939a.

The assimilation of these nutrients is an essential part of the synthetic processes which produce the organic matter which supports all life in the sea. It is essential, therefore, not to lose sight of the products of the syntheses and their variations with different environmental conditions.

Various analyses have been made of the carbon, nitrogen, and phosphorus content of both phyto and zooplankton. On the average, their composition closely resembles that of the sea water from which the nutrients were assimilated. The data are, however, far too incomplete to know whether there are consistent differences between species, or whether seasonal variations in composition of the plankton occur. Additional information on the composition of natural collections of planktonic algae is greatly to be desired.

Some indirect indications of possible variations can be obtained from analyses of pure cultures of algae. The carbon, phosphorus and nitrogen content of 6 species of algae which were grown in bacteria free cultures are shown in Table 1 (Ketchum & Redfield 1938; Ketchum, Lillick & Redfield Ined.). For each 100 parts of carbon the nitrogen content varies between 12.2 and 15.4 parts and the phosphorus content between 3.3 and 8.7 parts. These algae were grown in identical media and the observed variations in their composition are, consequently, not the result of any variations in their chemical environment. They may, thus, be attributed to the physiological differences in the species of algae studied.

TABLE 1. Composition of various fresh water algae grown in pure cultures.

Species	Parts by Weight		
	Carbon	Nitrogen	Phosphorus
Stichococcus bacillaris	100	13.8	3.33
Chlorella pyranoidosa	100	12.4	5.87
Chlorella vulgaris	100	14.5	5.51
Scenedesmus obliquus	100	13.8	8.73
Scenedesmus basilensis	100	15.4	6.69

Variations in the composition of algal cells may also be the result of growth in an unbalanced medium. The data in Table 2 show that *Chlorella pyrenoidosa* grown in the absence of nitrate and phosphate in the medium developed deficiencies in these elements within the cell. When the medium is again enriched with these elements the cells are able to assimilate them rapidly to make up their deficiencies. This assimilation is not dependent upon photosynthesis, since it can also occur, though at a slower rate, in the dark. As would be expected, the cells containing the least nitrogen were grown under conditions where their phosphorus supply was ample but their nitrogen supply was restricted. Conversely, the cells containing the least phosphorus were grown in a solution containing an adequate supply of nitrogen but no phosphorus (Ketchum 1939a).

TABLE 2. Variations in the composition of *Chlorella pyrenoidosa* as the result of growth in media deficient in phosphate and nitrate.

Experimental Treatment	Parts by Weight		
	Carbon	Nitrogen	Phosphorus
Normal *Chlorella* culture	100	12.4	5.89
Deficient *Chlorella* culture	100	5.9	2.12
Recovery, Phosphate added	100	4.0	3.76
Recovery, Nitrate added	100	16.2	1.15
Recovery, both added	100	13.9	4.48

Since it is known that the nitrogen and phosphorus content of the sea water varies between wide limits during the period of phytoplankton growth it is possible that cells deficient in these elements may be produced. Further data are necessary, however, to show just how great the changes in natural populations may be. Until this is known it is not possible to calculate exactly the productivity of ocean waters by determining the quantity of nitrogen or phosphorus removed from the water by the growth of the phytoplankton.

The regeneration of the nutrients in the sea is the result of two major biological processes. The plants may be consumed by animals and a portion of the nutrients is then excreted either in organic or inorganic form. The bacterial regeneration of nutrients acts directly on the dissolved organic materials in the water or upon dead plant or animal tissues. The net result of these two processes is to return the essential elements to the water in a usable form. The nutrients regenerated in the surface water, where there is adequate light for photosynthesis, are directly assimilated, and start the cycle again. Those regenerated in deeper water must await transport to the surface by vertical water motion.

It has been impossible to duplicate the natural rates of bacterial decomposition in the laboratory. As soon as a sample of natural water is enclosed in a bottle an enormous increase in the bacterial population develops. The rates of regeneration under these conditions are clearly of little direct application to the conditions which obtain in the sea. The fundamental character of the changes, however, can be studied. It has been found, for example, that when glucose is added to sea water, it is oxidized by the bacteria, and phosphate and nitrate are removed from the sea water in the process. Large additions of glucose, therefore, require enrichment of the water with these elements if the oxidation is to be carried to completion. If complete plant or animal material is added, on the other hand, the ample supplies of phosphorus and nitrogen are present in organic form, and are liberated in inorganic form as a result of the decomposition (Waksman & Carey 1935, Waksman & Renn 1936).

Both phosphorus and nitrogen may be liberated first as soluble organic compounds. The availability of such materials for assimilation by the plant cells is not known. All of the inorganic compounds of nitrogen, however, are readily assimilated by the plant and there is some indication that ammonia, which is produced first in the decomposition of nitrogenous organic matter, can be assimilated somewhat more easily than nitrate or nitrite (Harvey 1940). The experiments of von Brand, Rakestraw and their collaborators (1937-1942) indicate that ammonia may be produced very quickly from particulate organic matter and this will be immediately available for assimilation. Under conditions in the sea the phosphate may be returned to the water more quickly than are the nitrogen compounds. The rates of these processes must influence the availability of these essential nutrients during much of the year at higher latitudes where the supply is seriously depleted during the summer.

In the study of the cycle of photosynthesis and decomposition in the sea, as evidenced by the essential nutrients, the three major processes mentioned above must be taken into consideration. To reiterate, these are the assimilation by plants, the regeneration, either through animal excretion or bacterial decomposition, and the transport because of vertical or horizontal water movement. The relative importance of these three may be shown by the study of the distribution of phosphorus in the Gulf of Maine by Redfield, Smith, & Ketchum (1937).

The phosphorus content of the water was separated analytically into three fractions. These were the inorganic phosphate, the phosphorus combined in dissolved organic material and the phosphorus in particulate matter which could be filtered from the sea water. The distribution of each of these three fractions of phosphorus with depth in May and in November is shown in Figure 3. The inorganic phosphate is the form available for assimilation by the plants. The particulate phosphorus includes that in the microscopic living organisms, as well as any which may be present in detritus. The dissolved organic phosphorus is a step in the decomposition of the organic matter. The cycle of phosphorus is thus from inorganic to particulate to dissolved organic to inorganic.

During the interval between these two measurements a considerable accumulation of dissolved organic phosphorus occurred throughout the entire water column. The numbers on the right hand side of the figures show the percentage of total phosphorus found in each quarter of the water column. These show that the surface layer is somewhat depleted of phosphorus, and that little net change occurred between the two measurements.

In order to interpret and evaluate the changes which took place between these two measurements it is necessary to establish the direction in which changes are possible.

(1) The synthesis of organic matter, which changes inorganic to particulate phosphorus, can occur only in the upper layers of the water where there is adequate light for photosynthesis. The upper 60 meters probably closely defines this depth, and is called the surface layer.

(2) Transport of phosphorus downwards can occur only in the particulate form by the sinking of dead and dying organisms.

(3) Vertical transport of phosphorus upwards can occur only as a result of eddy diffusion of inorganic phosphate across the concentration gradient in the upper water layers.

(4) Decomposition of particulate to dissolved organic, and from the latter to the inorganic form can take place at any depth in the water column.

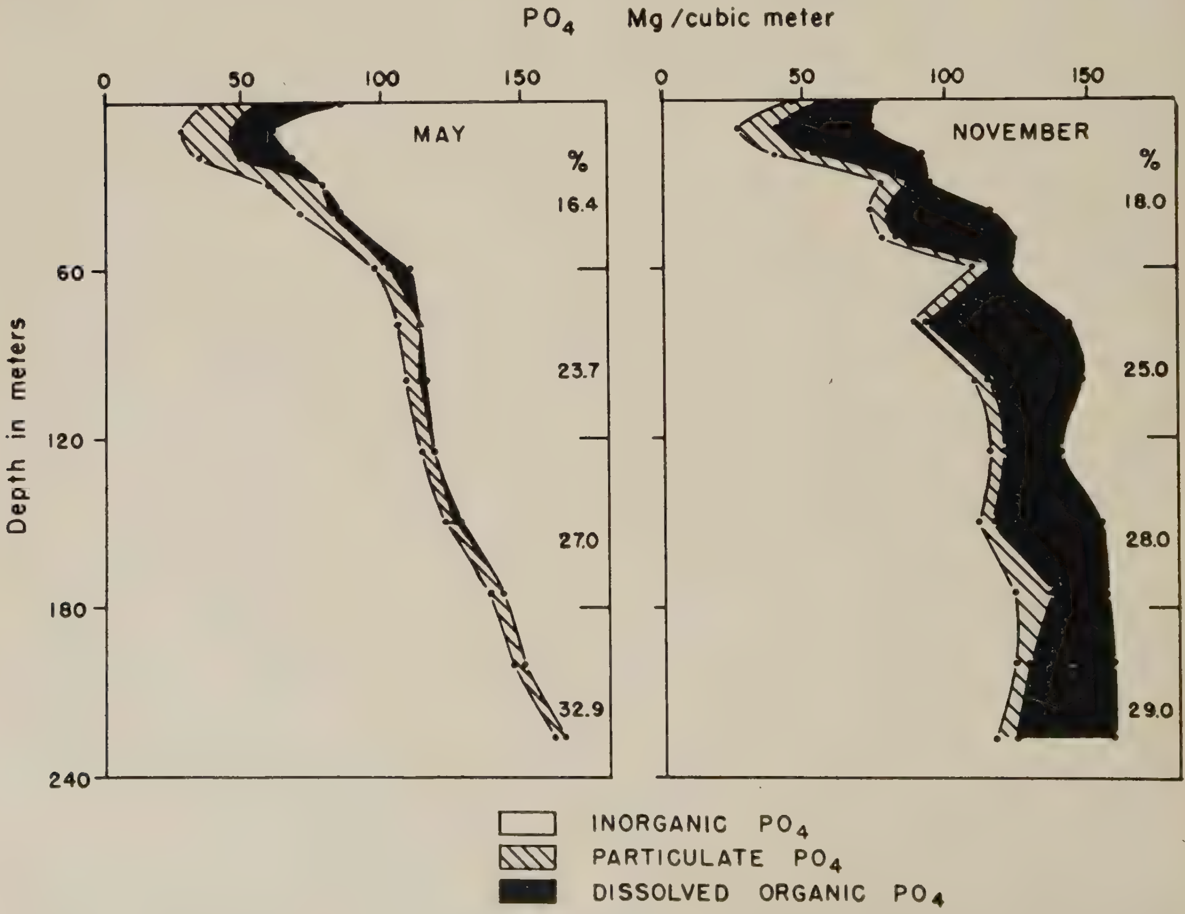

FIG. 3. The distribution with depth of inorganic, particulate and dissolved organic phosphorus in May and November in the Gulf of Maine.

In addition to these conditions which determine the direction in which the changes can occur it is also necessary to assume that horizontal transport may be neglected. This is never strictly true, and is approximately true only if the location is surrounded by a large area of similar water. The properties of a closed system have been artificially imposed upon our observations, however, by calculating all changes as percentages of the total.

The seasonal variation in the three fractions of phosphorus in the surface layer are shown in Figure 4. The period we are considering, between May and November, is the period of greatest photosynthetic activity, when inorganic phosphate is depleted in the surface waters. Even in midsummer, however, the total phosphorus in the surface layers is a substantial part of maximum amounts ever found there, though it is mostly present in combined organic form. The lower part of this figure shows the distribution of phosphorus with depth throughout the year. The phosphorus in the upper quarter of the water column varies from about 15 to 22% of the total phosphorus. When all of the fractions of phosphorus are considered, therefore, it is clear that the surface layers at this location are never exhausted of this nutrient, though a large proportion of the supply is combined, and is not available for assimilation by the plants. The conversions and rate of supply of available phosphorus must determine the fertility of the region.

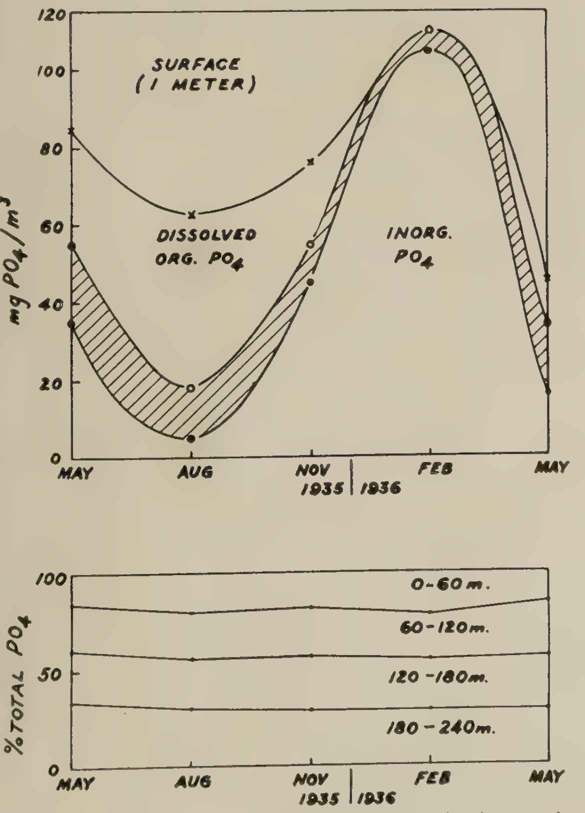

FIG. 4. Above: The seasonal changes in inorganic, particulate and dissolved organic phosphorus in the surface waters of the Gulf of Maine. Below: The proportion of total phosphorus in each quarter of the water column throughout the year.

The net changes in total phosphate between the May and November observations are small. There was a net gain of only one-half a gram of phosphorus by the surface water and a net loss of one-half a gram by all of the water below 60 meters. The total changes in the various fractions of phosphate are diagrammed in Figure 5. The deeper waters have gained more than 5 grams of organic phosphate most of which appears in the dissolved organic form. This must have been contributed by the sinking of particulate matter into this zone and its subsequent partial decomposition. To compensate for this gain there has been a slightly greater loss of inorganic phosphate. Since inorganic phosphorus can be utilized in synthetic processes only in the surface layers this must have been carried upwards in inorganic form by eddy diffusion and mixing. It was not found, however, in the surface layer which actually showed a slight decrease in inorganic phosphate during the same period. It must, therefore, have been assimilated by the plants and synthesized in organic matter.

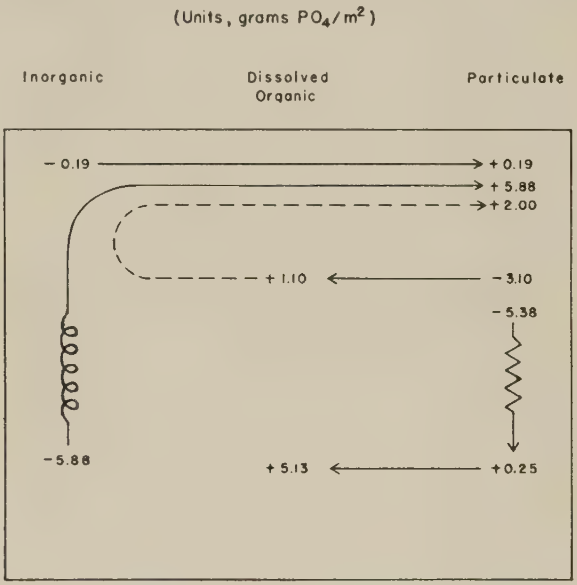

FIG. 5. Diagrammatic presentation of the conversion of phosphorus in the Gulf of Maine between May and November.

There is no direct way of measuring the amount of decomposition and regeneration of organic material which occurred in situ in the surface layers. There was, however, an increase of more than a gram in the amount of dissolved organic phosphate in this layer and this must have been derived directly or indirectly from the particulate material. In order to complete the picture an estimate has been made of the amount of material which may have completed the cycle of decomposition and re-assimilation in the surface layer. This estimate is based upon the rate of decomposition which was observed during the hundred days following the November observations when plant activity was at a minimum. At the end of this time, in February, it was found that a considerable decrease in organic phosphorus compounds had occurred throughout the water column with a compensating increase in inorganic phosphate. The rate of disappearance of the organic phosphorus observed in the upper 60 meter layer was 11.5 milligrams per day. This corresponds to a regeneration during the period of May to November of two grams. Although this estimate is obtained indirectly it is probably nearer the truth than to postulate that no decomposition took place within the layer because that part of the cycle which has gone to completion cannot be detected.

The fact that part of the cycle which has gone to completion is lost results in minimum estimates for the various changes in the cycle. For example, the effect of adding a quantity X to any step of the cycle results in no change in the net gains and losses of the system so long as the quantity, X, is carried through the complete cycle of vertical transport, synthesis and decomposition.

That the quantitative aspects of the cycle are not unduly under-estimated, however, can be shown by comparison with other results which were obtained by different methods. Seiwell (1935) calculated the production of organic carbon in the tropical Western North Atlantic to be 278 grams of carbon/sq. meter/year. This calculation was based on the assumption that the oxygen minimum layer of the mid-Atlantic is caused by the oxidation of organic matter produced in the overlying water. Redfield (1942) has shown that a considerable part of the oxygen is utilized in the oxidation of organic matter formed at the surface in higher latitudes. Seiwell's estimate of local production is thus too high. Seiwell estimated that the plankton produced would require the vertical transport of 7.56 grams of phosphorus. This would be equivalent to 20.8 mg/sq. meter/day. Riley's (1941) figures for the organic production on George's Bank vary from 140 to 950 mg of carbon/sq. meter/day during a period from April to September. If one assumed a "normal" carbon to phosphorus ratio of 100:2.5 the phosphorus assimilation during this period ranges from 3.5-23.2 mg P/sq. meter/day. Our values of 10.3 for vertical transport or of 14.2 mg/sq. meter/day for total utilization are within these limits obtained by independent methods of estimation.

It is clear from this description that it is impossible to define the total changes which take place in one of the essential plant nutrients without considering all of the processes which contribute to its distribution. The proportions of phosphorus supplied by the various processes is of interest. The total assimilation during this period is calculated as 8.07 grams per square meter. Of this, only a little over 2% disappeared from the original inorganic phosphate in the surface water layer, 73% was brought to the surface by vertical transport, and, it is estimated on meager grounds, which, however, are the best available at present, almost 25% was supplied by decomposition within the surface layer. It is only by considering the entire picture, and the various processes involved, that the whole story can be discerned.

Rather than close on too optimistic a picture of the problem, however, I would like to enumerate a few points concerning which our present information is altogether too meager.

(1) The knowledge of the composition of the natural populations of plankton is entirely too scanty to permit generalizations. The use of conversion factors which interrelate the various chemical, physical and biological properties of the populations will increase and be made more useful as the accuracy of the conversion factors improves.

(2) Direct evidence on the rate of decomposition of naturally occurring organic matter in the sea is greatly to be desired. If all of the other processes were known this could be inferred, of course, from the observations. The possibility of direct measurements in an isolated body of water should not, however, be overlooked.

(3) More accurate knowledge of the forces which control vertical mixing and transport of water are certainly desirable. This process, after all, accounted for 73% of the supply of phosphorus to the surface water in our observations, and it is the one factor most frequently neglected in studies of aquatic populations. The variations in the magnitude of these mixing processes with depth and stability of the water, with the seasons and the associated climatic changes, with wind and tidal currents must be more completely understood before the observed changes can be thoroughly explained.

When these additional pieces of the puzzle are available it will be possible to construct a balance sheet of the changes of any bio-labile element in the water with greater assurance than is possible at present.

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Contribution No. 378

MECHANICAL CONTROL OF SHIP-BOTTOM FOULING BY MEANS OF AIR BUBBLES[1]

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During the year 1943 investigations were carried out for the purpose of determining the effect of water currents upon the attachment of fouling organisms to submerged surfaces. As a result of these experiments it was demonstrated that a comparatively low water velocity applied continuously would prevent fouling (Smith, 1946). In the case of the species of barnacles most prevalent at Miami, a velocity of slightly more than one knot was sufficient to prevent attachment. It was also shown that barnacles which have been allowed to attach and remain undisturbed for a period of six hours are washed from their hold by currents in the order of 2½ to 3 knots.

Following these experiments attention was given to he manner in which water currents might be directed over a ship's hull, propellers or external portions of the sound apparatus for the purpose of preventing fouling. Dr. I. G. Slater of the British Admiralty Delegation advanced the suggestion that the necessary current might be produced by air bubbles. Experiments were initiated to determine whether it was in fact possible to inhibit fouling in this manner and subsequently to determine its economic practicability.

Since the completion of these experiments attention has been drawn to U. S. Patent No. 2138831, December 6, 1938, granted to F. G. Branner, relating to the use of gas bubbles released below ship's hulls for the purpose of preventing attachment of fouling organisms (Branner, 1937). Nothing in the specifications, however, suggests that the device has been subjected to biological investigation.

Acknowledgments are due to Mr. Martin Graham for assistance in preparing panel tests, to Mr. Leonard Wirtz for advice and help in preparing a service test installation, and to Mr. Charles Weiss for kindly preparing photographic illustrations.

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[1] These experiments were conducted while the author was engaged by the Woods Hole Oceanographic Institution in investigations under contract with the Bureau of Ships, Navy Department, which has given permission to publish the results. The opinions contained herein are those of the author and do not necessarily reflect the official opinion of the Navy Department or of the Naval service at large.

[2] Contribution number 16 from the University of Miami, Marine Laboratory.

Contribution No. 378
from the
Woods Hole Oceanographic Institution

Panel Tests

Glass panels 8″x12″ in size were submerged at an angle of 45 degrees, with the upper edge a few inches below and parallel to the surface of the water. In order to insure the known optimum conditions for the attachment of fouling organisms, black Cararras glass was used. Included in the floating frame containing the experimental panels were untreated control panels. The experimental surfaces were subjected to air bubbles by means of perforated plastic tubes situated close to the lower edges and connected to an air compressor (Figure 1). Results are shown in the photographs and are summarized in Table I.

The first test consisted of an untreated control panel, and two panels each subjected to air bubbles along a 3½ inch length of the base. At the base of one of the latter the bubbles were liberated from comparatively large holes about 1/16 of an inch in diameter and 1 4 inch apart. In the case of the other the holes were smaller, approximately 1/32 of an inch in diameter and 1/8 of an inch apart. Air released from the holes was measured by means of an inverted graduate and funnel. From the time required to fill the graduate the rate of air flow from the perforated 3½ inch lengths of tubing was calculated as approximately 0.4 and 0.2 cubic feet per minute for large and small bubbles respectively. Converted to units of cubic feet per minute per foot of perforated tubing these rates of flow are 1.3 and 0.6. Following a 48 hour period of exposure, beginning on May 18, the panels were examined for cyprids and metamorphosed barnacles. The number of these observed upon the control was 239. Upon the panel subjected to the smaller bubbles 85 barnacles had attached, but were confined to that half of the panel not subjected to bubbles. The remaining panel, subjected to the larger bubbles, had acquired 74 barnacles on the untreated half and the clear area extended well to one side of the bubble treated half.

The experiment was allowed to continue for a further 7 days before the panels were removed and photographed. It was observed that whereas heavy fouling had occurred upon the control (Fig. 1c), the treated surfaces were free of barnacles, and that in the case of the large bubbles the protected area was somewhat wider than the 3½ inch perforated length of tube at the base of the panel (Fig. 1a).

Since the results of the first test indicated beyond doubt that the attachment of fouling organisms might be prevented by air bubbles, a second test was designed to determine the minimum rate of airflow required to produce the anti-fouling effect. Three panels were used in this test, with airflows of approximately 1.3, 0.6 and 0.2 cubic

TABLE I

Effect of Air Bubbles upon Fouling of Glass Panels

Series and Experiment	Date Started	Air Flow in Cu. Ft. per min. per foot	Diameter of Perforations	Distance between Perforations	Exposure Period	Observations
I (a)	5–18–44	1.3	1/16″	1/4″	2 days	No cyprids
(b)		0.6	1/32″	1/8″	2 days	No cyprids
(c)		Control	....	....	2 days	Many cyprids
(a)		1.3	1/16″	1/4″	9 days	No fouling. Clear area extends beyond length of perforated tube.
(b)		0.6	1/32″	1/8″	9 days	No fouling
(c)		Control	....	....	9 days	Fouling
II (a)	7–10–44	1.3	1/32″	1/4″	14 days	No fouling
(b)		0.6	1/32″	1/4″	14 days	No barnacles. Bryozoa grow in from side.
(c)		0.2	1/32″	1/4″	14 days	Completely fouled
III (a)	7–24–44	0.6	1/32″	1/2″	25 days	No barnacles. Bryozoa grow in from side.
(b)		0.6	1/32″	1″	25 days	Same
(c)		Control	....	....	25 days	Completely fouled
IV (a)	9– 8–44	0.6 (Stopped daily for 4 hours)	1/32″	1″	18 days	Scattered barnacles
(b)		Control	....	....	18 days	Heavy fouling.

feet per minute per foot, respectively, liberated as bubbles through 1/32 of an inch diameter holes spaced at 1/4 of an inch intervals over a length of 3 inches. At the end of 14 days exposure the set of bubbles released most slowly was found to have permitted attachment of barnacles. Nevertheless, barnacles were less numerous over the bubble treated area than over the untreated edges of the panel. The two remaining panels were free of barnacles over the area covered by the bubbles. In the case of the most rapidly released bubbles the unfouled area extended beyond the 3 inch length of perforated tubing. The panel with the intermediate rate of bubbling showed growth of bryozoa inwards from the fouled area into the unfouled area. In all three panels a thin slime film formed towards the edge of the clear area but was less marked in the middle of the area or nearer to the source of the bubbles. The results of this series indicate that the minimum rate airflow required for anti-fouling lies between 0.2 and 0.6 cubic feet per minute per linear foot.

A third experiment was carried out to test the possibility of using bubbles spaced at wider intervals. Perforations of the copper tubing beneath one panel were 1/2 inch apart, and beneath a second, 1 inch apart. The holes were 1/32 of an inch in diameter and covered a length of six inches. Rate of airflow was 0.6 cubic feet per minute per foot in both cases. A third panel remained untreated as a control. At the end of 25 days exposure the control was heavily covered with barnacles, tunicates and bryozoa. The other panels were free of barnacles and tunicates, but some filamentous bryozoa had begun to grow in from the sides. It appeared that bubbles spaced at 1 inch intervals were as effective as when spaced at 1/2 inch intervals.

The effect of intermittent bubbling was investigated by means of panels similar to those used in previous experiments. The perforations were 1/32 of an inch, spaced 1/2 inch apart, and extended the width of the panel. The rate of airflow was about 0.6 cubic feet per minute per foot. On each day during the test the air was turned off for a period of four hours. The experiments was continued for a period of 18 days before removal from the water for examination. Whereas the untreated control panel had accumulated heavy fouling, the panel subjected to the intermittent flow of bubbles had only a few scattered barnacles upon its surface. These were of various sizes and had apparently attached during the entire period of he experiment. These results indicate that some of the barnacles which had attached during a four hour period not subjected to air bubbles were still able to develop when the air bubbles were resumed (Fig. 2).

The small number of these may indicate that only the more hardy are able to survive under these conditions. Although cyprid attachments were low on other test panels during the period of this experiment, a comparison of the experimental and control panels shows that had the intermittent bubbling not been effective a far greater number of barnacles would have attached during the daily four hour period and have developed than actually occurred.

Service Tests

In order to demonstrate the bubble method and in order to investigate the practical difficulties which might be encountered in applying it to the actual protection of ships' bottoms, service tests were carried out upon the University of Miami Marine Laboratory motor vessel, the *Nauplius*. The vessel is a 29 foot fast cabin cruiser, fitted with twin engines and capable of speeds in the order of 20 knots. Immediately behind the bow the sides of the hull arise at an angle close to the vertical At the stern the hull is almost horizontal with a slope of approximately one in eighteen. It was thus possible in using this vessel to test the effect of bubbles on hull surfaces at widely varying angles to the vertical. A false keel 2″x 2″ in cross section was fitted to the vessel and to each side of this were fastened 1/2″ copper tubes, running the length of the vessel and passing vertically upwards at the stern to the deck where regulating valves and air hose attachments were arranged (Fig. 3). The copper tubes were perforated over a length of 12 feet at the after end of the portside and for a distance of 12 feet at the forward end of the starboard side. The holes were spaced at 1/2″ intervals and were 1/32 of an inch in diameter. Air was supplied from a one-half horsepower compressor, delivering 2 to 3 cubic feet per minute. Old paint on the bottom was burned off and a light green topside paint applied. Immediately after launching the compressor hose was attached to the vessel and air bubbles were applied to the hull. The compressor was inadequate for the purpose and difficulties arose, owing to the variation in depth of the keel below the water line. As a result of this, air was liberated more readily from the higher parts of each of the two tubes. Bubbles were therefore confined to areas of the hull extending over the after 3 or 4 feet on the portside and over a similar distance on the starboard side immediately forward of amidships. Air was applied continuously whenever the *Nauplius* was moored in dock.

The experiment continued for a period of five weeks, during which the vessel was used for various purposes at sea. When not lying at her dock the air hose attachment was removed immediately before getting under way. The speed of operation varied between 10 and 20 knots, except when plankton nets or other trolling equipment was being used. When away from her dock the vessel was not allowed to remain stationary for periods of more than a few minutes. At the end of the exposure period the *Nauplius* was hauled and the bottom examined. Although fouling was substantially reduced on the portions of the hull subjected to air bubbles, nevertheless barnacles were scattered over these surfaces. It was particularly noted that even over the almost horizontal portion at the stern, air bubbles had afforded as much protection as over the more steeply inclined portion amidships. Propeller struts obstructed bubbles and caused fouling beyond.

A second test was carried out upon the same vessel, using a more powerful compressor. This was operated by a 3 horsepower motor and delivered 15 cubic feet per minute. The same arrangement of copper tubes and perforations was used. Other conditions were essentially the same as in the previous experiment.

At the end of three weeks the vessel was again hauled (Figs. 3, 4 and 5). The contrast between protected and unprotected areas was greater than in the previous experiment, and the bubbles had covered a greater area of the hull. Nevertheless, at the deepest part of the hull, lying between the bow and midship section, bubbles had not been released, and fouling had occurred. A length of 2 feet immediately behind the bow had also become fouled due to failure of the bubbles to be released from the forward end of the copper tube (Fig. 5).

It was demonstrated by the foregoing results that air bubbles, when released at the keel at a sufficient rate, provided anti-fouling protection. At the same time it was demonstrated that the varying depth of the keel caused an unequal distribution of bubbles, resulting in a lack of protection above the lowest points of the keel.

Discussion

The results of the panel tests indicate quite clearly that submerged surfaces may be protected by means of air bubbles. Service tests on the M.V. *Nauplius* also demonstrate that the protection applies equally well to flat bottom hulls as well as to bottoms arising more sharply.

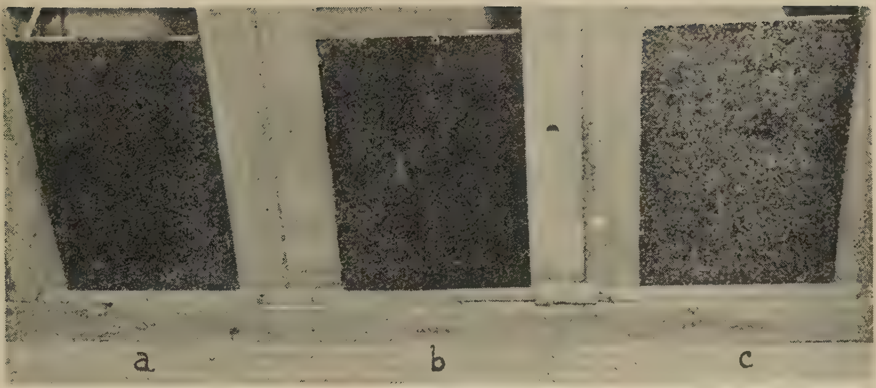

Figure 1.

(*a*) Panel subjected to 1.3 cubic feet of air per minute per foot, liberated from perforations 1/16 of an inch in diameter, 1/4 of an inch apart in 3 1/2 inches of panel width. Exposed 9 days.

(*b*) Similar, but with air flow 0.6 cubic feet per minute per foot.

(*c*) Control panel with no air bubbles.

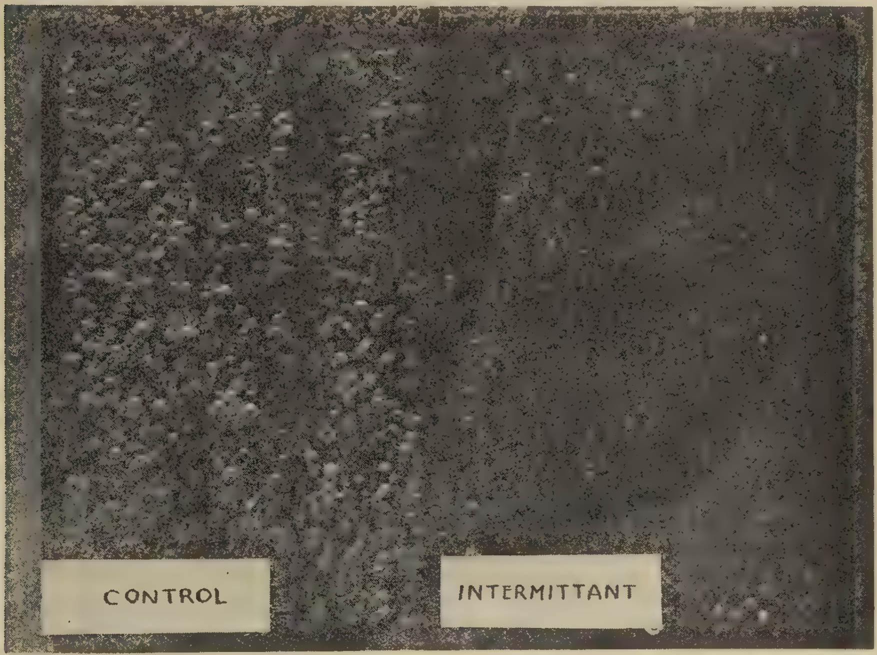

Figure 2.

(*Right*) Panel subjected to bubbles for 20 hour periods alternating with 4 hour periods of rest. Airflow 0.6 cubic feet per minute per foot liberated from 1/32 of an inch diameter perforations, 1 inch apart. Exposed 18 days.

(*Left*) Control.

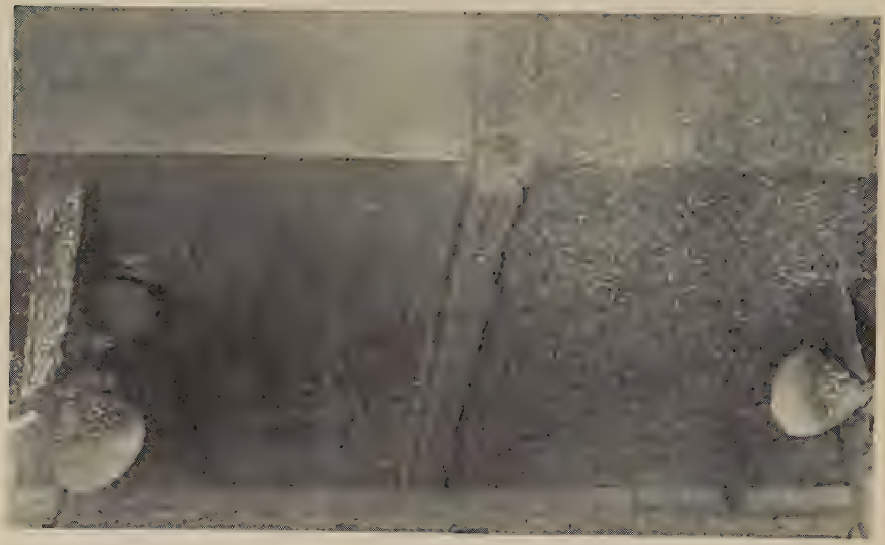

Figure 3.

Stern of M.V. *Nauplius* showing air tubes. Bubbles released on port (left) side of keel only. Three weeks' test using 3 h.p. compressor.

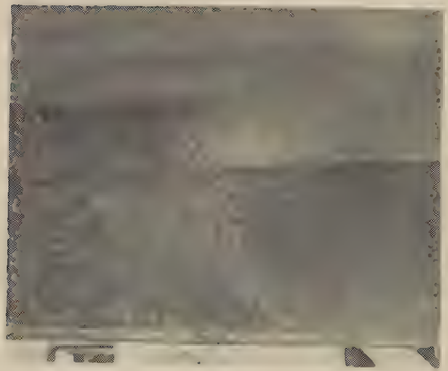

Figure 4.

Portion of bottom amidships from starboard showing untreated area at left (sternwards) and area subjected to bubbles at right (forwards). Same conditions as Figure 3.

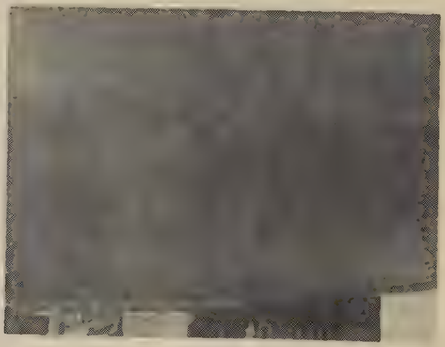

Figure 5.

More general view amidships, similar to Figure 4, but showing fouling due to lack of bubbles toward the bow.

The panel experiments have also shown that holes as small as 1/32 of an inch in diameter and as far apart as 1 inch will provide a sufficient flow of air bubbles.

Of more importance from a practical point of view is the actual volume of air required to protect a vessel, and the power needed to provide this. From the second and third panel tests results were obtained which showed a flow of 0.6 cubic feet per minute to be ample protection for each horizontal foot of the ship's bottom. It is possible that as little as half of this would be sufficient since the next lowest rate of flow which was found to be unsatisfactory was 0.2 cubic feet per minute per foot. Nevertheless, even were a rate of 0.3 cubic feet per minute per foot satisfactory it would necessitate a total of 18 cubic feet per minute in order to cover both sides of the bottom of a 30 foot vessel. For this purpose a four horsepower compressor would be required. With larger vessels the power necessary to provide air bubble protection would increase not only with the length of the vessel but also with the depth of the keel, though to a lesser extent.

The problem of discontinuity of air bubble release with varying keel depth remains to be solved. The solution may lie in separate treatment of sections of the bottom according to the depth of the keel. Bilge keels and similar projections would necessitate auxiliary tubing.

The possibility of using intermittent bubbling has not been clearly proved by the panel test. Were this possible the power needed for protection of the hull might be cut down by a system of treating several sections of the hull alternately.

A suggestion by Dr. Slater that the anti-fouling effect of the air bubbles might be due to action upon the attached young of fouling organisms rather than through production of water currents raises theoretical questions. Nothing observed in the foregoing experiments offers evidence on this point. Although it might be argued that the protection of a flat bottom must be due to some direct mechanical action upon the attached young of fouling organisms rather than through production of water currents raised theoretical questions. Nothing observed in the foregoing experiments offers evidence on this point. Although it might be argued that the protection of a flat bottom must be due to some direct mechanical action of the air bubbles, yet it was observed that the bubbles rose from the edges of the flat bottom as quickly as from other portions of the hull and could quite possibly have created as strong a water current along the bottom.

The service tests show that it might be possible to prevent fouling of ships' bottoms by liberating air bubbles from the keel whenever the ship lies at rest. Further analysis of the results may show that the amount of power needed would render this impracticable. There are special situations, however, where it is believed the use of this method may be very satisfactory. External portions of the sound detecting equipment and such special devices as pitot-tube logs upon which it might not be desirable to apply anti-fouling paint could very readily be protected by a system of air bubbles.

Summary

Previous experiments have demonstrated that water currents of comparatively small velocity suffice to prevent the attachment of fouling organisms. The present investigations were designed to test the possibility of producing these currents upon ship's hulls by means of air bubbles liberated below the keel.

Preliminary experiments were carried out upon submerged glass panels. It was found that complete protection could be afforded by means of bubbles liberated from the base of the panels.

Under the conditions of the experiment barnacles were not merely prevented from growing but were unable to attach as cyprids.

Further experiments demonstrated that an air flow of less than 0.6 but greater than 0.2 cubic feet per minute per horizontal foot of surface was necessary to prevent attachment of fouling organisms. It was found that perforations in the air tube might be as small as 1/32 of an inch in diameter and as far apart as 1 inch without reducing the efficiency of protection.

Intermittent release of bubbles consisting of 20-hour active periods followed by 4 hour periods without bubbles did not afford complete protection although considerably less fouling occurred than on control panels.

Service tests were carried out upon a 30 foot vessel, with air bubbles liberated from both sides of the keel. These tests resulted in satisfactory anti-fouling protection so long as an adequate air flow was maintained. Both flat bottoms and bottoms arising at an angle from the keel were equally protected.

It is suggested that although the amount of air required may render the method impracticable for entire hulls, yet on sound domes and other under-water equipment where anti-fouling paint may not be desirable, air bubbles offer a simple and efficient anti-fouling measure.

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Contribution No. 382

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Tidal Illumination Diagrams

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THE TIDAL ILLUMINATION DIAGRAM IS one of the various graphic devices designed during the recent war to represent significant hydrographic conditions on military targets. It was introduced by the Oceanographic Section of Headquarters, Army Air Forces, in 1942 to represent relationships between stage of the tide and state of illumination in target areas of Northwest Africa. Later, its use was extended to all theaters, and preparation on a mass scale was taken over by the U. S. Coast and Geodetic Survey, where facilities are available for computation and graphic presentation of these data for many parts of the world. Recent comments have shown the diagrams to be of practical use in this postwar period.

The tidal illumination diagram is so arranged that for any hour of the day combinations of solar illumination and stage of the tide are readily noted. Heights of high and low tides are referred to the sound datum of nautical charts of the specific locations. In so far as possible, tidal data from the U. S. Coast and Geodetic Survey tide tables are used. The occurrences of high and low tides are shown as a series of connected points enabling the user to visualize the changing sequence throughout the month. Days of the month are represented by vertical lines covering the period from noon through midnight to noon of the next day.

Three types of twilight are indicated to bring out gradation in light from sundown to darkness and from darkness to sunrise. Civil twilight begins with sunset and ends when the sun is 6° below the horizon. During this period, objects may be distinguished readily, and a newspaper may be read without the aid of artificial light. At its end, sky brightness is approximately 20 times that of the full moon at zenith (Fig. 1). In the following period of nautical twilight, the brighter stars are visible, the horizon is

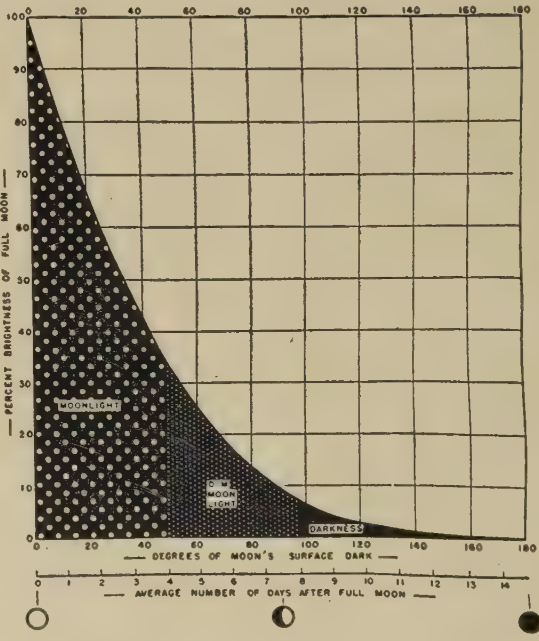

FIG. 1. Relative brightness of moon with change of phase.

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[1] Contribution No. 382.

generally indistinguishable, but general outlines of objects not too distant can be distinguished. Astronomical twilight begins when the sun is 12° below and ends when it is 18° below the horizon. During this period, illumination is distinctly brighter than during complete solar darkness but less than during periods of dim and brilliant moonlight (Figs. 2 and 3).

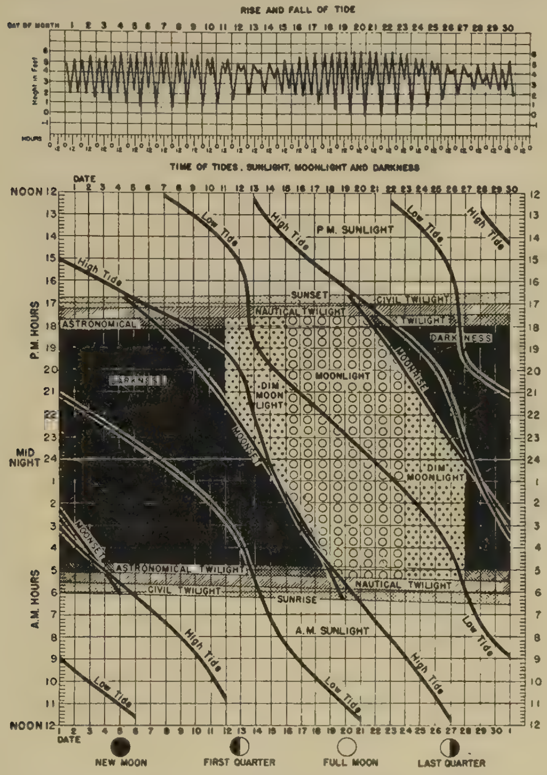

FIG. 2. Tidal illumination diagram for Yokohama, Japan, at time of occupation, November, 1945.

Variations in moonlight intensity are arbitrarily divided into periods of bright and dim moonlight. Bright moonlight is taken as the period from four days before to four days after the appearance of full moon, during which time light intensity varies between full moon brightness at its zenith and about one-third of this value (Fig. 1). The period of dim moonlight includes four days prior to the beginning of bright moonlight and four days after its end, during which time illumination intensity varies from about one-third to about one-tenth of full moon brightness at zenith. The relative brightness of the moon with phase is illustrated by Fig. 1.

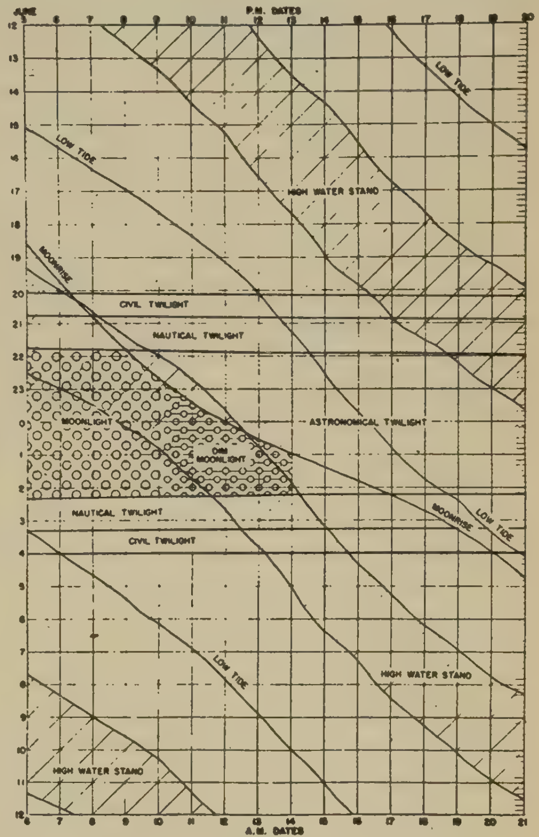

FIG. 3. Tidal illumination diagram for "Omaha" Beach, Normandy, France, during invasion, June 1944.

Tidal illumination diagrams for important target areas of World War II are illustrated by Figs. 2 and 3. These can be prepared for any coastal area where tides have been predicted; their usefulness lies in the prognosis of future conditions as well as in historical studies.

Contribution No. 383

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COMMENTS ON P. A. SHEPPARD'S DIRECT MEASUREMENT OF GROUND STRESS

By R. B. MONTGOMERY
(and reply by P. A. SHEPPARD, B.Sc., F.Inst.P.)

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Comments on P. A. Sheppard's direct measurement of ground stress

Sheppard's (1947) measurement of the wind stress on a horizontal plate simulating ground is a welcome advance in the study of atmospheric turbulence, because all previous estimates of the stress between air and ground have been based on less direct forms of evidence. Measurements of the mean wind speed at several levels in the lowest two meters of air accompanied the measurements of stress and enabled him to compute "Kármán's constant" or the "universal turbulence constant"; the average obtained from three satisfactory runs with slight or moderate hydrostatic instability is 0·46.

Where the mean wind speed u is proportional to the logarithm of the nondimensional height z/Z, z being height and Z being any constant length, the universal turbulence constant κ may be defined by

$$\frac{\partial u}{\partial ln\,(z/Z)} = \frac{u^*}{\kappa} \quad . \quad . \quad . \quad . \quad . \qquad (1)$$

The quantity $u_* \equiv (\tau/\rho)^{\frac{1}{2}}$, τ being shearing stress and ρ being density, is assumed to be independent of height in this formulation. Integration from level 1 to level 2 gives

$$\frac{u_2 - u_1}{u_*} = \frac{1}{\kappa}\, ln\, \frac{z_2}{z_1} \quad . \quad . \quad . \quad . \quad . \qquad (2)$$

This is the equation used by Sheppard for determining the turbulence constant from measured values of τ, ρ, z_1, z_2, u_1, u_2.

A value of about 0·40 has commonly been used for the turbulence constant. As previously pointed out (Montgomery 1943), the value resulting from application of Kármán's mixing-length theory to Nikuradse's measurements in tubes is only 0·31. Kármán's theory, however, is not entirely appropriate for tubes; it fails completely in the axial region. The geometrical mixing-length hypothesis which I introduced is intended to permit measurements with long tubes to be correctly applied to problems of flow over large plane surfaces. It is intended to fit both geometrical shapes with the same turbulence constant; this cannot reasonably be expected of Kármán's theory, which is basically incompatible with conditions in a tube. The new hypothesis leads, above a plane boundary, to the usual linear mixing-length distribution and, within a circular cylinder, to a distribution that agrees excellently with Nikuradse's tube measurements mentioned by Sheppard if the turbulence constant equals 0·45. The close agreement between this value and Sheppard's 0·46 appears at first to lend support to both determinations.

Sheppard's three runs, however, give quite different values of the turbulence constant, so the average 0·46 is not a sufficiently reliable determination to warrant any confidence being placed in the preceding close agreement. The measured wind speeds are plotted in Fig. 1. All but two points fall close to a straight line for each run, so the wind speed appears to be proportional to $ln\,(z/Z)$. From the slope of each line a value of the turbulence constant can be computed from equation (1), the value of u_* being obtained from value of stress and density tabulated by Sheppard. The results are found to differ from the individual values of the turbulence constant tabulated by Sheppard, as follows:

Run	1	2	3
u_*, cm. sec.$^{-1}$	15·9	12·9	12·5
κ, Sheppard	0·45	0·44	0·49
κ, recomputed	0·37	0·44	0·54

The discrepancy for run 1 results because the top point was included by Sheppard but is omitted in the recomputation. Sheppard's value for run 3 appears to be in error; if equation (2) is used for each of the three intervals of height, as was done by Sheppard, the results are 0·53, 0·40, 0·85; the average of these is 0·59, not 0·49. Since the recomputed turbulence constant ranges from 0·37 to 0·54, an average value based on these measurements cannot be considered an accurate determination. Sheppard, indeed, claims no great accuracy, for he states 0·46 "to be in good agreement with Nikuradse's value of 0·40."

The positions as well as the slopes of the lines in Fig. 1 are of interest. If, according to equation (2), z_0 is the value of z_1 at which $u_1=0$, equation (2) becomes, with the subscript 2 omitted,

$$\frac{u}{u_*}=\frac{1}{\kappa}\,ln\frac{z}{z_0} \quad . \quad . \quad . \quad . \quad . \qquad (3)$$

The quantity z_0 is the "roughness length." Each straight line in Fig. 1 intersects the line $u=0$ (outside the diagram) at the ordinate $ln\,(z_0/Z)$. The resulting values of the roughness length are 2×10^{-3} cm. for run 1, 3×10^{-4} cm. for run 2, and 4×10^{-5} cm. for run 3. In comparison, the roughness length that follows from Kármán's velocity distribution above a hydrodynamically smooth surface is $z_0=v/(\kappa u_*)$, where v is the kinematic viscosity (see Rossby, 1936, equation 16); the value given by this formula is about 2×10^{-3} cm. for all three runs. The observed velocity distribution in run 1 therefore conforms closely with Kármán's except at the top point. Runs 2 and 3, however, give roughness lengths even smaller than that previously considered to correspond to a hydrodynamically smooth surface.

The mixing length l may be defined by $u_*=l\partial u/\partial z$. Since the kinematic eddy viscosity K is defined by $\tau\equiv K\rho\partial u/\partial z$, mixing length and eddy viscosity bear the relation $K=lu_*$ A logarithmic distribution of wind is seen to be accompanied by linear distributions of mixing length and eddy viscosity. Sheppard's Fig. 5 showing mixing length determined from the average of the three runs is misleading: the 13 plotted points were obtained graphically from a smoothed curve and represent observations for only 3 intervals of height; the greater than linear increase of mixing length above 1 m. is due to the two points which have been neglected in drawing the straight lines in the present Fig. 1. On the basis of further (unpublished) evidence, however, Sheppard comes to the important conclusion that in lapse conditions the mixing length at higher levels exceeds a linear distribution, while in inversions it is less than the linear distribution. Sverdrup (1936, p. 48) found the same result for inversions over a snow surface.

Sheppard's (1947, pp. 215-6) tentative conclusion that the turbulence constant varies with stability may be questioned, as he points out, because the definition of the turbulence constant fails wherever the logarithmic wind distribution fails, as it does in both stable and unstable conditions. Under stable or unstable conditions the turbulence constant is defined only in a shallow surface layer having logarithmic wind distribution. A variation of the turbulence constant would be at variance with Sverdrup's conclusion: "Under stable conditions the eddy convectivity very near the surface has the same value as in the case of indifferent equilibrium, other conditions being alike, but it increases more slowly with elevation."

It is to be hoped that the studies initiated by Sheppard will be carried forward. One desirable addition is a demonstration that the measured force on the artificial disc is an accurate representation of the shearing force on the same area of ground.

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Contribution No. 383.

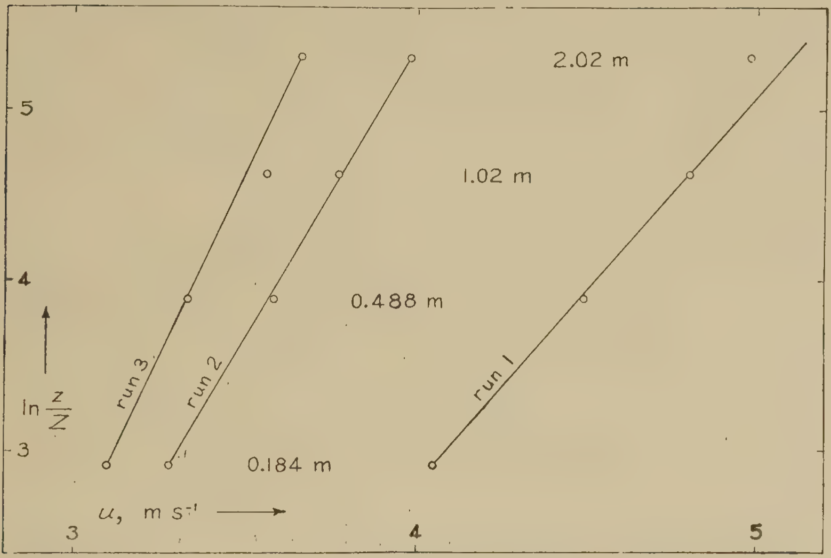

Fig. 1.—Graph of Sheppard's (1947) observations of wind speed u against natural logarithm of z/Z, where z is height and $Z=1$ cm.

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A reply to Dr. Montgomery by Asst. Professor P. A. Sheppard.

The main point of Dr. R. B. Montgomery's note appears to be that my measurements of surface drag in association with the velocity profile, and hence von Kármán's constant κ, cannot be used to distinguish between one or another of the various values of κ which have been proposed from the analysis of laboratory measurements of fluid flow. I entirely agree, and for two reasons:

(*a*) the accuracy of my measurements of drag and of the velocity profile in a natural wind whose intensity and scale of turbulence was necessarily many times that in a pipe cannot be expected to match that attainable in the laboratory where the drag can be measured with very great accuracy by a simple, but indirect method, namely from the pressure gradient in the pipe.

(*b*) the atmospheric measurements were complicated by the effects of hydrostatic instability.

In spite of the obvious difficulties which would attend any measurement of κ in the lower atmosphere, the central position of this constant in modern empirical turbulence theory made the attempt seem worth while to the writer, particularly as the intensity and scale of turbulence in the lower atmosphere are so much greater than are normally encountered in other fields of turbulent flow. Further, it had been suggested that the κ concept, might only be applicable to the atmosphere with a value much enhanced over that appropriate to pipe flow—a suggestion, however, for which the writer could find no sympathy. The development of the necessary technique took some time and was only perfected shortly before the last war with the result that the work had to be abandoned before the desirable long series of observations could be obtained. Its resuscitation at this time is hindered by many factors, not least that the special and extensive concrete surface on which the observations were made is no longer available.

Montgomery has recomputed κ from my observations of drag and of the velocity profile and claims a wider actual dispersion than given in my original paper (though the mean of his three re-computed values, 0·45, agrees with my original mean value). But he does this by entirely neglecting one point out of four in two of my three velocity profiles and I cannot accept this arbitrary procedure. The neglected points depart from Montgomery's lines by 11 cm.sec.^{-1} for Run 1 and 6 cm.sec.^{-1} for Run 3 and these departures are certainly greater than the experimental error. Further their neglect removes a characteristic feature from the profiles of velocity taken in unstable hydrostatic equilibrium, *viz.* a convexity of the u, log z curves towards the u-axis. (This characteristic and a corresponding characteristic of concavity towards the u-axis in stable equilibrium will be dealt with more fully in a later paper.) Nevertheless some latitude in the most appropriate value of κ from each run does exist and, as indicated in my first paragraph above, I do not consider my values to be of the accuracy required to distinguish definitely between, say, $\kappa = 0{\cdot}40$ as derived from the initial slope of Nikuradse's mixing-length profiles and the more recent value of 0·45 suggested by Montgomery from a generalisation of the mixing-path theory of turbulence. I am, however, inclined to think that the initial slope of my mean mixing-path profile, *viz.* 0·45, *observed in moderately unstable conditions*, lends a little weight to a lower value than 0·45 for κ in neutral equilibrium, for which condition only is κ strictly defined.

The difficulty in obtaining a reliable value for κ, in the laboratory as well as in the field, arises from its definition. Thus von Kármán (1930) defined κ (Montgomery's nomenclature above is used) as

$$l = \kappa \frac{\partial u/\partial z}{\partial^2 u/\partial z^2}$$

with

$$l = u_*(\partial u/\partial z)^{-1}$$

Thus

$$\kappa = u_* \frac{|\partial^2 u/\partial z^2|}{(\partial u/\partial z)^2}$$

and the difficulty arises from the difficulty in obtaining an accurate value of the second derivative of the velocity profile. The fact that κ is obtained in practice from an integrated form of the last equation, *e.g.* from Montgomery's equation (2) for flow over a plane boundary, where u_* may be accurately assumed independent of height, should not be allowed to hide this aspect. Montgomery's (1943) treatment (of which I was not aware when I prepared my original paper) is a welcome attempt to obtain a sound value for κ from observations in tubes, where u_* varies linearly with distance from the tube wall, but it is made at the expense of introducing a purely empirical form for the mixing path, distance relation.

I thoroughly agree with the penultimate paragraph of Dr. Montgomery's note. But I believe that the variation of κ with temperature gradient which I gave in my original paper may serve a practical purpose in this respect, that, if the transfer of any property from the earth's surface, *e.g.* evaporation or heat flux, be calculated from observations of the corresponding profiles *assumed logarithmic*, κ must be adjusted to the departure of the temperature gradient from the dry-adiabatic lapse rate.

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Contribution No. 384

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LIFE TABLES FOR NATURAL POPULATIONS OF ANIMALS

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(Contribution No. 384 from the Woods Hole Oceanographic Institution)

> At sperat adulescens diu se victurum, quod sperare idem senex non potest. Insipienter sperat; quid enim stultius quam incerta pro certis habere, falsa pro veris?
>
> —Cicero, *De Senectute*

INTRODUCTION

"THE certainty of death", remarks Sir Thomas Browne, "is attended with uncertainties, in time, manner, places." The same refrain, audible in classical authors from Horace to Hoffenstein, embodies immutable truth. But the rise of life insurance has taught us to ask the fatal question differently. We now substitute "probability" for "certainty," and have exchanged our fates for parameters of populations. The dictum of Galilei, "to measure what can be measured, to make measurable what can not be measured," has been applied to the product of Lachesis' loom, with interesting results.

There is no evidence that man's maximum life span has been lengthened a particle since antiquity. The celebrated cases of fantastic longevity, from Methuselah to Thomas Parr, do not withstand critical scrutiny. The mean length of life, however, differs widely among the races of men, is notably lower for most primitives than for civilized populations, and has been increasing by leaps and bounds in the United States during the last century. In ancient Rome, according to Macdonell's analysis (1913), the expectation of life at age 10 was an additional 22 years, compared to an additional 55 years for a male resident of the United States in 1929–31 (Dublin and Lotka, 1935).

The Romans, in fact, knew more about such matters than might be supposed from their superstition that "ten times twelve solar years were the term fixed for the life of man, beyond which the gods themselves had no power to prolong it; that the fates had narrowed the span to thrice thirty years, and that fortune abridged even this period by a variety of chances, against which the protection of the gods was implored" (Hodge, 1857, cited from Niebuhr's *History of Rome*). A table showing the expection of life at birth, at age 20, and at 5-year intervals thereafter, evidently based on real experience and intended for the computation of annuities, was in use in the third century A.D.; it is attributed to Ulpian (Trenerry, 1926). Even the Babylonians seem to have known about insurance contracts, though this does not necessarily imply any actuarial knowledge, and Horace's reference to "Babylonian numbers"—"Tu ne quaesieris (scire nefas) quem mihi, quem tibi finem di dederint, Leuconoe, nec Babylonios temptaris numcros" (*Odes*, I: 11)—may mean more than he intended.

Having gained some idea of the limits circumscribing his own mortality, man has turned to look at the other animals. In 1935 Pearl and Miner, in their discussion of the comparative mortality of lower organisms, attempted to formulate a general theory of mortality. They quickly gave up the attempt upon realizing that the *environmental* determinants of life duration can not, at least as yet, be disentangled from such *biological* determinants as genetic constitution and rate of living. They ended with a plea for "more observational data, carefully and critically collected for different species of animals and plants, that will follow through the life history from birth to death of each individual in a cohort of statistically respectable magnitude." Thus by implication Pearl and Miner appealed to the ecologists, who for the most part have been busy elsewhere. Accounts of the conceptions and methodology of life tables have not yet found their way into textbooks of ecology, and while field naturalists have devoted increasing attention to the dynamics of natural populations most of them have been content to leave the construction of life tables to the statisticians and laboratory ecologists.

This article, which is designed as an introduction to the subject rather than as a formal review, brings together from the ecological literature a mass of information bearing on the survival of animals in nature. This information has not heretofore been considered relevant by biometricians working with human populations, nor has it ever been considered in its context by ecologists. In collecting the material it was immediately obvious that it is still too early to formulate general theories. Serious deficiencies are only too apparent in the data. But the difficulties differ from case to case, and are therefore not insurmountable. Moreover, the bibliography will show that virtually all of this knowledge has been acquired in the twelve years since the appearance of the review by Pearl and Miner. By taking stock now, and by calling attention to gaps in our information, it is hoped that some guidance can be given to ecologists and others in the gathering of new material.

THE MEANING OF THE LIFE TABLE

A life table is a concise summary of certain vital statistics of a population. Beginning with a cohort, real or imaginary, whose members start life together, the life table states for every interval of age the number of deaths, the survivors remaining, the rate of mortality, and the expectation of further life. These columns are symbolized by d_x, l_x, q_x and e_x, respectively, where x stands for age. Additional columns which may be tabled include the age structure (L_x) or the number of persons living who are between ages x and $x + 1$.

Because all the life table functions can be calculated from each other, it makes little difference where one begins in summarizing the method of construction. It is convenient to begin with deaths at given ages (d_x), since these usually make up the "raw data." A curve obtained by plotting number of deaths against age is obviously a histogram showing the frequency distribution of deaths. It is customary to reduce the data to a relative basis by expressing the observed number of deaths at any age as a fraction of the total number of deaths. Such fractions stated as percentages and carried out to three figures include a decimal place; in this review and elsewhere where small samples are involved, it is the practice to drop the decimal point and put deaths, etc., on a "per thousand" basis. Starting, then, with a cohort of 1000 individuals born together, survivorship (l_x) is obtained by successive subtraction of deaths in the age interval from survivors at the beginning of the age interval. Mortality rate (q_x) is the fraction of those living at the beginning of the age interval who die during the interval, $q_x = d_x/l_x$, and is usually expressed here on a per thousand basis, $1000\ q_x = 1000\ d_x/l_x$.

The calculation of expectation of life is more complicated. For individuals at age 0 (at the beginning of their life span), it is the same as the mean length of life of the cohort. For older individuals, it is the mean life span remaining to those attaining a given age. It could therefore be calculated for any age x by measuring the area under the survivorship curve beyond x and dividing by the number of survivors attaining age x,

$$e_x = \frac{\int_x^\omega l_x \cdot dx}{l_x}$$

However, a life table, among other things, is a device for obtaining such integrals arithmetically, being divided into age intervals so small that changes between age x and $x + 1$ can be regarded as linear functions of x. It is therefore assumed that the *age structure*, L_x, or the number of persons alive who are between ages x and $x + 1$, which is exactly given by

$$L_x = \int_x^{x+1} l_x \cdot dx$$

is in practice given by

$$L_x' = \frac{l_x + l_x + 1}{2}$$

Successive values of L_x obtained in this way are then summed from the bottom of the column up to each age x. This gives T_x, the total number of (persons $\times$ age units), or person-years if age is expressed in years still to be lived by persons of age x. Dividing by l_x, the number of persons, gives the expectation of life in age units,

$$e_x = \frac{T_x}{l_x}$$

Farner (1945) calculates e_x directly for each year of a bird's age by obtaining the mean after lifetime of birds alive on their first November 1, doing the same for birds alive on their second November 1, and so on. This procedure is cumbersome, and is more accurate than the method given here only if the deaths in any year are so unequally distributed through the year that a serious error results from ignoring the fact (Lack, 1943b).

Nice (1937) gives, as Table XXVIII, the "theory as to age composition of a population of breeding birds; theoretical numbers of each age according to annual survival rate." As this table has been frequently used by students of bird populations, it is as well to understand its construction. Actually, it consists of a group of life table d_x columns, constructed on the assumption of mortality rates which are *constant with respect to age*, but change from column to column between 75 and 25 per cent per year. It may seem surprising that a table of deaths should show the age composition of the living, but this is merely a consequence of starting with a round number of births, 100 in this case. Nice takes a cohort of 100 individuals and obtains their survivorship by successive applications of the assumed mortality rate until the number of survivors is reduced to 1. She then expresses the number living at any age as a percentage of the total number living at all ages, and thus the age composition of the living becomes identical with the number of deaths. For the ratio of the living at any age to the total number living must equal the ratio of the dead at any age to the total number of deaths,

$$\frac{l_x}{\Sigma l_x} = \frac{d_x}{\Sigma d_x}.$$

But $\Sigma d_x = 100$, by convention; therefore

$$100 \frac{l_x}{\Sigma l_x} = d_x.$$

By the same reasoning it can be shown that

$$100 \frac{L_x}{\Sigma L_x} = dx.$$

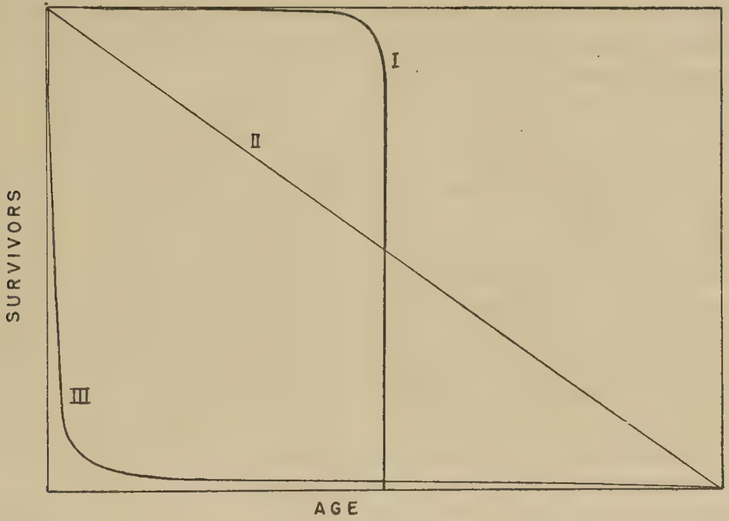

FIG. 1. SCHEMATIC REPRESENTATION OF THEORETICAL TYPES OF SURVIVORSHIP CURVE, ADAPTED FROM PEARL AND MINER (1935)

The survival axis can be graduated either arithmetically or logarithmically, but the logarithmic scale is more instructive, in that a straight line implies equal *rates* of mortality with respect to age.

Nice's table is convenient for ornithologists, since the assumption of constant age-specific mortality rates proves to be approximately true for adult birds. When mortality rates change with age, as they normally do, the table is inapplicable, though of course the age composition computed as percentage will always bear the same relationship to the d_x column. Nice states that her table applies to species breeding at one year of age, but this is not a necessary condition, as Farner (1945) has pointed out: it merely implies that the birth rate cannot be deduced from the life table age composition unless all members of the population breed every year.

The fact that the various life table columns are interconvertible makes it unnecessary to discuss all of them in dealing with a given species. Usually it is sufficient to focus attention on the survivorship curve, since this is most readily comprehensible. Pearl and Miner (1935; see also Pearl, 1940) have made it clear that there are three possible sorts of distribution of survivorship with respect to age, as shown diagrammatically in Fig. 1. Type I, the *negatively skew rectangular*, is shown by members of a cohort which, having been born at the same time, die more or less simultaneously after a life span which is presumably characteristic of the species. Type II is *diagonal* (when the logarithm of the number of survivors is plotted against age), implying a constant mortality rate for all age groups, or no one age as a favored time of dying. Type III, the *positively skew rectangular*, shows extremely heavy mortality beginning early in life, but the few individuals which survive to advanced ages have a relatively high expectation of further life.

Most survivorship curves hitherto published, including those for man, *Drosophila*, *Hydra*, *Agriolimax*, the mouse (Pearl and Miner, 1935), the vole (Leslie and Ranson, 1940), the black widow spider (Deevey and Deevey, 1945), *Tribolium* (Pearl Park, and Miner, 1941), and other laboratory animals, are variants of the diagonal type, or rather are intermediate between Type I and Type II. Type III has never been obtained with a laboratory population, though marine species with pelagic eggs and larvae, such as the oysters, would doubtless fall here if complete data were available. Type I has been observed in the case of adult *Drosophila* which were given no food, but this sort of survivorship is probably to be thought of as a laboratory curiosity.

KINDS OF LIFE TABLES

Life tables for human populations, which differ in certain important respects from animal populations in nature, are calculated by roundabout methods, most of which have little relevance to ecology. Some understanding of them is nonetheless essential. Census data show the number of persons born in a given year living in various political areas. Published vital statistics give the number of deaths in the same areas each year and the ages of those dying. By combining the two sets of figures it is possible to arrive at estimates of the rate of mortality (q_x) suffered by persons of a given age *at the time of the census*. Using a smooth curve fitted with exquisite precision to the q_x data, a life table can be constructed on the assumptions: (1) that a standard cohort (100,000 persons) is born alive uniformly throughout the year of the census; (2) that its members will be exposed throughout life to these particular mortality rates; and (3) that there is no immigration or emigration.

A life table so derived exposes to view a purely theoretical population, one which might have existed at the time of the census, but which ceased to exist even before the census was complete. For human populations are notably subject to immigration and emigration; the best known ones are growing, and their age structure is therefore changing; and what is even more important, the mortality rates observed at the time of the census are certain to change with the passage of time. An example will make clear how ordinary life table procedure crystallizes an imaginary population from a series of "time-specific" death rates.

This example is a paraphrase of Merrell's lucid exposition delivered at the symposium on "Life Tables and Their Application" held at Boston on December 27, 1946.

In 1940 the individuals, born in 1890 and now living in a certain state, were exposed to a risk of death at their current age (50 years) which works out at 12.58 per thousand. By 1950 the survivors of these same individuals, now aged 60 years, will be exposed to a different risk of death, say 27.03 per thousand. Eventually the last survivor will be dead, having been subject, in his last year of life, to a mortality rate of 1000 per thousand, and at that time it will be theoretically possible to construct a survivorship curve for the original group of individuals born in the state in 1890 and suffering age-specific mortality rates which changed systematically throughout their lives. But this will be impossible to do in practice, since (1) the birth records for 1890 are incomplete, and (2) many of those whose births were recorded will have left the state and died elsewhere. Moreover, (3) they will have been replaced by a number (probably a larger number) of persons born elsewhere in 1890, subjected to different mortality risks for varying fractions of their lives, who appear in the death records merely as "born in 1890."

In 1940, however, we also know the mortality rate for individuals born in 1900, and now 40 years of age. By 1950, when these persons are 50 years old, their age-specific mortality rate at age 50 will be obtainable. It will not be 12.58 per thousand, but probably a slightly lower figure. In fact, the mortality rates for all ages will have changed slightly, some more, some less, by 1950, partly because of immigration and emigration and partly because of improvements in public health technique. The same applies, mutatis mutandis, to 1960, when the 1900 year-class are 60 years old. In actuarial practice *this does not matter*. By drawing a vertical line, as it were, through all the age-classes present in 1940, and taking their age-specific mortality rates as the basis of a life table, the actuary seizes the only way out of a troublesome situation. He erects a hypothetical population and tables its survivorship, its mortality rates, its age structure, and the expectation of life of its members, and his figures serve for ordinary purposes. In any case they are the best available until the next census, when they have to be completely revised.

A very different life table would result if, instead of arbitrarily halting the flow of events at some particular time, as 1940, we followed all the individuals born in a certain state in a particular year, and recorded their deaths as they occurred. This would be a "horizontal" life table. Human biologists are less interested in this type, for from their standpoint, life being long and patience short, it is more worth while to be able to predict the future than to describe the past. The life table for persons born in 1840 is not of pressing concern to medical scientists (or to insurance salesmen) in 1940, conditions having meanwhile changed profoundly. The two sorts of life table approach identity as the age structure of the population approaches stability in a uniform environment, but these considerations have no real meaning to the actuary, who deals with expanding populations in which births exceed deaths and which are constantly improving their own environmental conditions. The ecologist, on the other hand, is bound to be interested in both kinds of life table. If there is no change in the environment from year to year, and if the natural population is at equilibrium, with recruitment of each age class always kept exactly balanced by deaths, a horizontal life table for the year-class born in 1940 or any other year will be identical with a vertical life table drawn up for all year-classes present in 1940 or any other year. But normally there will be good years and bad years, both the birth rate and the age-specific death rates will oscillate more or less reciprocally, and the resulting differences in the two sorts of life tables will be large.

Since the data necessary for a vertical life table include both a census of the age distribution of the living members of the population and a record of the deaths by ages, the horizontal life table is easier to construct. The experimental ecologist, in particular, can go at the problem directly, by allowing a large cohort to be born at the same time, keeping its members under observation throughout their lives, and recording deaths as they occur. Thus survivorship (l_x) and deaths (d_x) make up the raw data of his experiment. Mortality rates are then easily obtained as the ratio of the dying to the living at any age, and other life table functions follow just as readily. The environment having been maintained constant artificially, there should be no difference between such a life table and one built up vertically from a census made when the age structure becomes stable.

ECOLOGICAL LIFE TABLES

The field ecologist deals with populations which are by no means so elementary as those inside *Drosophila* bottles. Even the total size of the population of a species cannot be easily ascertained for an area large enough to be representative, and calculations of the birth rate and death rate are uncertain at best, largely owing to immigration and emigration. It is seldom indeed that the ecologist knows anything of the age structure of a natural population. In a few cases, growth rings on the scales or otoliths (fish) or horns (ungulates) make it possible to determine the age of an animal: Moore (1935) has shown that annual growth rings occur in the genital plates of sea-urchin tests, as they do in the shells of some molluscs. Moore checked the validity of the age determination by reference to the size-frequency distribution in his catches, and the separation of modal size classes in a population often affords a clue to age, particularly for younger age groups. The age of adult females can be determined in the case of certain mammals (whales, Wheeler, 1934, Laurie, 1937; seals, Bertram, 1940) by counting the corpora lutea in the ovaries. But for most animals it is possible to find out the ages of individuals only by marking them in some way.

Even when the age of a member of a natural population is known, it is not a simple matter to obtain accurate vital statistics. The source of greatest confusion lies in the impracticability of keeping the individuals under continuous observation. Migratory birds, for example, are easy to band as nestlings, but nearly impossible to find between fledging and the time they leave for winter quarters. Often they can not be found at all unless they return to the same area to breed, when they can be trapped in nest boxes. Their mortality between fledging and breeding can be calculated, but the calculation is rendered uncertain by the tendency of young birds not to return to their birthplaces as breeding adults.

As sources of data for the construction of life tables, the ecological information falls into three groups: (1) cases where the age at death (d_x) is directly observed for a large and reasonably random sample of the population; (2) cases where the survival (l_x) of a large cohort (born more or less simultaneously) is followed at fairly close intervals throughout its existence; (3) cases where the age structure is obtained from a sample, assumed to be a random sample of the population, and d_x is inferred from the shrinkage between successive age classes. It should be noticed that only the second sort of information is statistically respectable, since in so far as the breeding can safely be assumed to be simultaneous, it is comparable to that obtained from a *Drosophila* bottle. The first and third types can be used only if one is prepared to assume that the population is stable in time, so that the actual age distribution and the life table age distribution are identical. This assumption would certainly not be true of a human population; it may be approximately true for many natural populations of animals. When it is definitely not true, e.g., when certain age classes are stronger or weaker than they should be, to take the ages at death or the actual age structure as observed at any "instant" of time will give erroneous estimates of the age-specific mortality rates. In these cases it would be better to construct a series of horizontal life tables, one for each year class. A vertical life table could be constructed from the average age composition observed over many years, if the ages at death were also known. But the ecological information does not yet give both the census by ages and the deaths by ages for any one population.

In making comparisons between species that have widely different life spans, Pearl's device is very useful. This consists in shifting the origin of the age axis from zero to the mean length of life and regraduating the age scale so that age is expressed as percentage deviation from the mean. In this way l_x values (and other life table functions, should they be desired) can be shown on the same graph in equal detail for rotifers, which live for a matter of days, and for birds, which live for many years. In connection with this method it has been customary to work with a fitted curve, the life table functions being calculated for equal percentage deviations, as -80%, -60%, -40%, etc. This procedure, applied to the natural populations considered in this review, would entail an enormous amount of arithmetical labor which does not seem to be justified by the end in view. Curve fitting minimizes observational error and generalizes the sweep of the observations, but in this case the generalization goes too far, in that it seems to confer a universality on the resulting life table which is not supported by the facts. The published life tables for *Drosophila*, the flour beetle, and other lower organisms apply only to the particular experimental conditions under which they were obtained. Under other conditions, e.g., with different population densities, the longevity will be different and different life tables will result. Accordingly, all life tables presented below have been treated simply, and age intervals, though expressed as percentage deviation from the mean longevity, have been entered in the tables only for values corresponding to the original observations. The only exception is the life table for *Balanus balanoides* (see footnote, Table 6).

Age at Death Directly Observed

In the course of his careful investigation of the wolves of Mt. McKinley, Murie (1944) picked up the skulls of 608 Dall mountain sheep (*Ovis d. dalli*) which had died at some time previous to his visit, and an additional 221 skulls of sheep deceased during the four years he spent in the Park. The age of these sheep at death was determinable from the annual rings on the horns. "Time, which antiquates antiquities, and hath an art to make dust of all things, hath yet spared these minor monuments" (Sir Thomas Browne, *Urn Burial*). Most of the deaths presumably occurred directly as a result of predation by wolves. Many skulls showed evidence of a necrotic bone disease, but it is not possible to say whether death was due solely to the disease or whether the disease merely ensured death by predation.

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The mean longevity of the later sample is significantly greater (7.83 years) than that of the earlier (7.09 years), but the interpretation of this fact is not clear. The form of the distribution of deaths is sensibly the same in the two samples. As the survival of the members of this population is astonishingly great, it seems best to be conservative, and attention has been focussed on the larger, earlier sample. Except for the "lamb" and "yearling" classes, which are doubtless under-represented in the data owing to the perishability of their skulls, there is no reason to suppose that either group is anything but a fair sample of the total population, i.e., the probability of finding a skull is not likely to be affected by the age of its owner. A life table for the 608 sheep has accordingly been prepared (Table 1). The survivorship curve, plotted logarithmically in Fig. 2, is remarkably "human" in showing two periods of relatively heavy mortality, very early and very late, with high and nearly constant survival ratios at intermediate ages.

TABLE 1

Life table for the Dall Mountain Sheep (Ovis d. dalli) based on the known age at death of 608 sheep dying before 1937 (both sexes combined). Mean length of life 7.09 years*
Data from Murie (1944)

x	x'	d_x	l_x	$1000\,q_x$	e_x
AGE (*years*)	AGE AS % DEVIATION FROM MEAN LENGTH OF LIFE	NUMBER DYING IN AGE INTERVAL OUT OF 1000 BORN	NUMBER SURVIVING AT BEGINNING OF AGE INTERVAL OUT OF 1000 BORN	MORTALITY RATE PER THOUSAND ALIVE AT BEGINNING OF AGE INTERVAL	EXPECTATION OF LIFE, OR MEAN LIFE-TIME REMAINING TO THOSE ATTAINING AGE INTERVAL (*years*)
0–0.5	−100	54	1000	54.0	7.06
0.5–1	−93.0	145	946	153.0	—
1–2	−85.9	12	801	15.0	7.7
2–3	−71.8	13	789	16.5	6.8
3–4	−57.7	12	776	15.5	5.9
4–5	−43.5	30	764	39.3	5.0
5–6	−29.5	46	734	62.6	4.2
6–7	−15.4	48	688	69.9	3.4
7–8	−1.1	69	640	108.0	2.6
8–9	+13.0	132	571	231.0	1.9
9–10	+27.0	187	439	426.0	1.3
10–11	+41.0	156	252	619.0	0.9
11–12	+55.0	90	96	937.0	0.6
12–13	+69.0	3	6	500.0	1.2
13–14	+84.0	3	3	1000	0.7

* A small number of skulls without horns, but judged by their osteology to belong to sheep nine years old or older, have been apportioned *pro rata* among the older age classes.

The adult sheep have two principal methods of defense against wolves, their chief enemies: flight to higher elevations, where wolves can not pursue; and group action or herding. It is clear that these recourses confer a relative immunity to death by predation and that only the very young, which have not learned by experience, and the very old, which are too feeble to escape, suffer heavy losses. This survivorship curve is decidedly not of the positively skew rectangular type.

The second case to be discussed is that of an aquatic invertebrate, the sessile rotifer *Floscularia conifera*. This species has been studied by Edmondson (1945) under conditions which are fully as natural as those enjoyed by Murie's mountain sheep. *Floscularia* lives attached to water plants, especially *Utricularia*, surrounded by a tube constructed by itself out of pellets of detritus. The tube is added to at the top continuously throughout life, and Edmondson was able to identify all the members of a population living in a pond by dusting the *Utricularia* plant with a suspension of powdered carmine. On subsequent visits the *Floscularia* present at the time of dusting were conspicuously marked by bands of carmine-stained pellets in the walls of their tubes, each band being surmounted by new construction of varying widths. Thus in one operation the stage was set for an analysis of growth, age, birth-plus-immigration, and death in a natural population. Among other spectacular results, Edmondson found that the expectation of life of solitary individuals was only half as great as that of members of colonies of two or more, and he presented separate life tables for each component of the population, calculated from the age at death. To facilitate comparison with other species, however, solitary and colonial individuals have been lumped together (for Edmondson's "Experiment 1") in the life table of Table 2.

The survivorship curve (Fig. 2), like that of the Dall sheep, shows unexpectedly good survival. As Edmondson has pointed out, it is not so good as that of other rotifers reared in the laboratory under standard conditions (*Proales decipiens*, *P. sordida*, *Lecane inermis*), but it is only a little less good, and life tables for these rotifers are notorious (Pearl and Miner, 1935) for their close approach to a Type I distribution.

TABLE 2

Life table for the sessile rotifer Floscularia conifera based on the known age at death of 50 rotifers, both solitary and colonial. Mean length of life 4.74 days
From Edmondson (1945), Experiment 1

x	x'	d_x	l_x	$1000\,q_x$	e_x
AGE (*days*)	AGE AS % DEVIATION FROM MEAN LENGTH OF LIFE	NUMBER DYING IN AGE INTERVAL OUT OF 1000 ATTACHING	NUMBER SURVIVING AT BEGINNING OF AGE INTERVAL OUT OF 1000 ATTACHING	MORTALITY RATE PER THOUSAND ALIVE AT BEGINNING OF AGE INTERVAL	EXPECTATION OF LIFE, OR MEAN LIFE TIME REMAINING TO THOSE ATTAINING AGE INTERVAL (*days*)
0-1	−100	20	1000	20	4.76
1-2	−78.9	200	980	204	3.78
2-3	−57.8	60	780	77	3.70
3-4	−36.7	0	720	0	2.98
4-5	−15.6	300	720	416	1.97
5-6	+5.4	140	420	333	2.02
6-7	+26.7	60	280	214	1.79
7-8	+47.7	140	220	636	1.14
8-9	+68.8	40	80	500	1.25
9-10	+90.0	20	40	500	1.00
10-11	+111.0	20	20	1000	0.50

The case of *Floscularia* is almost above reproach as an example of a life table obtained under natural conditions. It is, of course, open to the objection that only the age at death is known, and the age structure of the living animals must be assumed to be constant. Apart from this deficiency, it should also be realized that the origin of the life table is not at birth. The pelagic larval life of the rotifer, like the larval life of barnacles and insects, is omitted from consideration in such a table.

A life table for a population of herring gulls (*Larus argentatus*) has recently been prepared by Paynter (*in press*). These gulls, banded as chicks at the Bowdoin Scientific Station, Kent Island, Bay of Fundy, have been recovered dead from all over North America. No special effort was made to recover banded gulls at their birthplace, and the colony is a large one (ca. 30,000 birds). The fact remains, however, that the first-year birds are perhaps more likely to be picked up than older birds near the place of banding, and perhaps less likely to be picked up elsewhere, so that some doubt can be cast on the reliability of the first-year recoveries as truly representative of the deaths in the first year. This troublesome point is probably less serious than with the songbirds to be discussed below; moreover, it is overshadowed by another difficulty, the fact that the study is not complete, and many of the banded birds are still alive. Paynter minimized this error by a compensatory adjustment; since banding began ten years ago and is still being carried out, first-year recoveries were divided by 10, second-year recoveries by 9, etc. Birds dying at ages greater than 10 years have naturally not yet been recorded, though a few are to be expected.

That these older birds will probably not change the life table appreciably is shown by Marshall's independent study (1947) of the longevity of the herring gull. Marshall used all available records of American herring gulls banded as young during the last 25 years and subsequently recovered dead. Thus his data probably include most of the returns from the Kent Island population. Returns before September 1 of the first year of life were excluded, so that the life table refers to adult birds only. It differs from Paynter's chiefly in that it includes birds older than 10 years, one bird having lived as long as 17 years. Despite two factors which might be supposed to enhance the apparent longevity (exclusion of juvenile mortality; inclusion of older birds) the expectation of life is markedly lower than that of the Kent Island colony, 1.5 years on the first September 1 of life as against 2.44 years at banding age.

Probably neither set of data for the herring gull is wholly reliable. Paynter's calculations suggest that the Kent Island population is just replacing its losses, assuming a rather high reproductive potential and a rather low rate of mortality between hatching and fledging, while a similar calculation applied to Marshall's figures implies that the population as a whole must be declining. Several reasons may be suggested for the discrepancy between the two life tables: (1) the mortality of the Kent Island gulls may actually be lower than average; (2) there may have been greater total mortality before 1936, and Marshall's recoveries may have been predominantly from the earlier years, before banding started at Kent Island. The simplest explanation is that (3) an appreciable number of bands are lost by older birds, so that the mean age at death is actually higher than appears from the returns of banded birds.

These questions will doubtless be discussed by Paynter on the basis of direct observation of juvenile mortality, planned for the coming summer (1947) at Kent Island. Meanwhile, taking his life table at face value, the figures have been entered in Table 3, and the survivorship curve is plotted in Fig. 2 for comparison with the Dall sheep and the rotifer. In contrast to those cases, the curve for the gulls is of the diagonal type, the mortality rate being approximately constant throughout life. This feature seems to be characteristic of birds, as will appear below. The causes of death of these birds have been discussed in detail by Paynter, who finds that there is no significant difference in mean length of life between gulls dying through human interference (shooting, trapping, etc.) and those dying through "natural" or unknown causes.

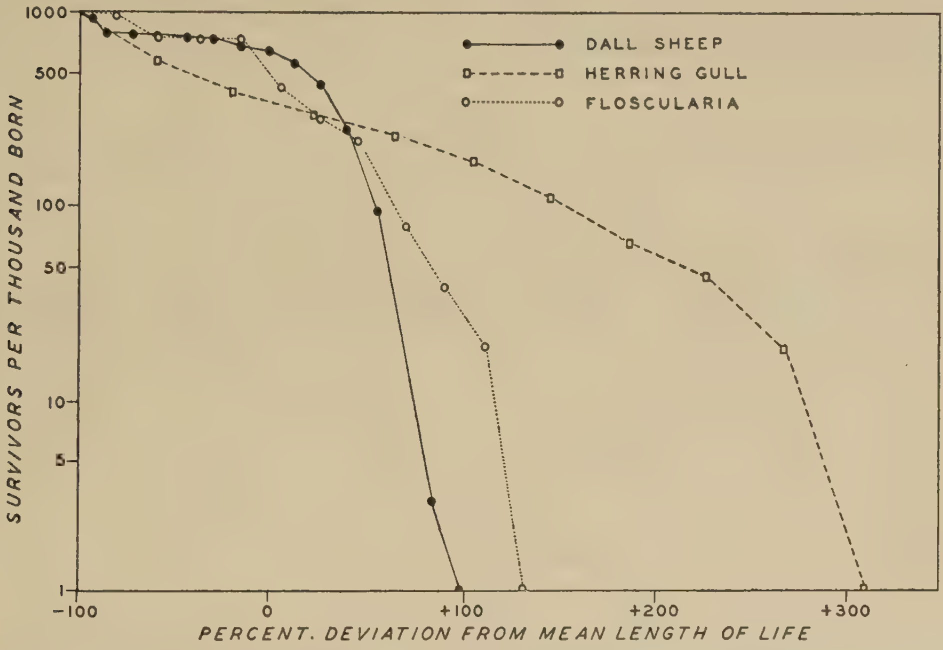

FIG. 2. SURVIVORSHIP (l_x) CURVES FOR THE DALL MOUNTAIN SHEEP, THE SESSILE ROTIFER FLOSCULARIA CONIFERA, AND THE HERRING GULL, AGE BEING EXPRESSED AS PERCENTAGE DEVIATION FROM THE MEAN LENGTH OF LIFE

In his delightful book, *The Life of the Robin* (1943a) and in two admirable papers, Lack (1943b,

c) has investigated the age at death of certain British birds, as obtained by recoveries of individuals banded as nestlings. Because banded nestlings are likely to be picked up near the banding stations or not at all, it is impossible to estimate the whole of the mortality in the first year of life with any accuracy, and Lack begins his life tables on August 1. The proportion of birds banded which are later recovered is small, ranging from 1.0 per cent for the robin to 18.4 per cent for the cormorant; but after August 1 of the first year it is considered that the ages at death of birds recovered are not likely to differ from the ages at death among the total population. The samples are small and of course become progressively smaller with increasing age, so that Lack does not regard the mortality rates and expectation of life as reliable beyond the fourth or fifth year.

TABLE 3

Life table for the Herring Gull (Larus argentatus) based on returns of 1252 birds banded as chicks at Kent Island, Bay of Fundy, 1936–1945. Mean length of life 2.44 years

From Paynter (in press)

x	x'	d_x	l_x	$1000\ q_x$	e_x
AGE (*years*)	AGE AS % DEVIATION FROM MEAN LENGTH OF LIFE	NUMBER DYING IN AGE INTERVAL OUT OF 1000 BORN	NUMBER SURVIVING AT BEGINNING OF AGE INTERVAL OUT OF 1000 BORN	MORTALITY RATE PER THOUSAND ALIVE AT BEGINNING OF AGE INTERVAL	EXPECTATION OF LIFE, OR MEAN LIFE TIME REMAINING TO THOSE ATTAINING AGE INTERVALS (*years*)
0–1	−100	419	1000	419	2.44
1–2	−59	181	581	312	2.84
2–3	−18	95	400	238	2.90
3–4	+23	65	305	213	2.65
4–5	+64	69	240	288	2.22
5–6	+105	60	171	351	1.92
6–7	+146	45	111	405	1.68
7–8	+187	21	66	318	1.48
8–9	+228	26	45	578	0.93
9–10	+269	19	19	1000	0.53

Several of Lack's life tables are reproduced in Table 4, and the survivorship curves are shown in Fig. 3. Three of the species are familiar British songbirds belonging to the Turdidae, the robin (*Erithacus rubecula melophilus*), the blackbird (*Turdus m. merula*), and the song thrush (*T. e. ericetorum*). The others are the starling (*Sturnus v. vulgaris*) and the lapwing (*Vanellus vanellus*), taxonomically though not ecologically a "shorebird" (Charadriidae). Lack's remaining species, the woodcock, black-headed gull, lesser black-backed gull, and cormorant, have been omitted, as they suffer more or less severe depredations from shooting.

The striking feature of these survivorship curves is their diagonal form. The mortality in the first year varies from 380 per thousand for the lapwing to 723 per thousand for the robin, but for a given species the mortality remains approximately constant throughout life, or at least for as long as the data are reliable.

When the ages of these birds are transformed into percentage deviations from the mean, as in Fig. 4, it becomes obvious that the mortality per unit of life span is constant for all the birds studied. This does not tell us anything new, for any series of diagonal lines will become the same when replotted in this way, but it is helpful none the less. A line fitted by eye to the survivorship points plotted in this figure has a slope corresponding to a mortality of about 320 per thousand per 100 per cent deviation. If the divergence of the points for older ages is ignored as being due to inadequate data, and this line projected, it cuts the age axis at about +560 per cent, implying that if the mortality of birds is really constant throughout life, the oldest bird in a group of 1000 adults should survive about 6.6 times as long as the average bird.

The American robin (*Turdus m. migratorius*), a larger bird than its distant English relative, has been studied by Farner (1945), using U. S. Fish and Wildlife Service data on 855 birds banded as young

TABLE 4

Life tables for several British birds, based on returns from all Britain of birds banded as nestlings and known to be alive on August 1 of their first year. Age reckoned from August 1

From Lack (1943a, b, c)

SPECIES; SIZE OF SAMPLE; MEAN LENGTH OF LIFE AFTER FIRST AUGUST 1	x	x'	d_x	l_x	$1000\ q_x$	e_x
	AGE (*years*)	AGE AS % DEVIATION FROM MEAN LENGTH OF LIFE	NUMBER DYING IN AGE INTERVAL OUT OF 1000 ALIVE ON AUGUST 1	NUMBER SURVIVING AT BEGINNING OF AGE INTERVAL OUT OF 1000 ALIVE ON AUGUST 1	MORTALITY RATE PER THOUSAND ALIVE AT BEGINNING OF AGE INTERVAL	EXPECTATION OF LIFE, OR MEAN LIFE-TIME REMAINING TO THOSE ATTAINING AGE INTERVAL (*years*)
Blackbird (352) 1.58 years	0–1	−100	545	1000	545	1.57
	1–2	−37	170	455	374	1.85
	2–3	+27	142	285	498	1.66
	3–4	+90	57	143	398	1.82
	4–5	+153	34	86	396	1.80
	5–6	+216	20	52	385	1.65
	6–7	+280	17	32	531	1.38
	7–8	+343	9	15	600	1.33
	8–9	+405	0	6	0	1.50
	9–10	+470	6	6	1000	0.50
Song Thrush (374) 1.44 years	0–1	−100	556	1000	556	1.44
	1–2	−31	185	444	417	1.61
	2–3	+39	136	259	525	1.40
	3–4	+108	72	123	585	1.39
	4–5	+178	21	51	411	1.65
	5–6	+245	13	30	433	1.43
	6–7	+316	11	17	647	1.12
	7–8	+385	3	6	500	1.17
	8–9	+455	3	3	1000	0.67
Robin (130) 1.01 years	0–1	−100	723	1000	723	1.03
	1–2	−2	131	277	472	1.41
	2–3	+97	108	146	740	1.23
	3–4	+196	23	38	605	2.29
	4–5	+294	8	15	533	4.0
	5–6	+392	0	15	0	3.0
	6–7	+491	0	15	0	2.0
	7–8	+590	0	15	0	1.0
	8–9	+689	8	7	1000	0.5
Starling (203) 1.49 years	0–1	−100	487	1000	487	1.49
	1–2	−33	261	513	509	1.43
	2–3	+34	113	252	448	1.40
	3–4	+102	89	139	640	1.12
	4–5	+168	25	50	500	1.22
	5–6	+236	20	25	800	0.92
	6–7	+302	0	5	0	1.60
	7–8	+370	5	5	1000	0.60
Lapwing (460) 2.36 years	0–1	−100	380	1000	380	2.37
	1–2	−58	213	620	344	2.51
	2–3	−15	128	407	314	2.56
	3–4	+27	78	279	280	2.50
	4–5	+70	67	201	334	2.28
	5–6	+112	56	134	418	2.17
	6–7	+154	24	78	308	2.37
	7–8	+196	20	54	370	2.20
	8–9	+239	7	34	206	2.20
	9–10	+282	9	27	333	1.63
	10–11	+324	7	18	389	1.17
	11–12	+366	11	11	1000	0.55

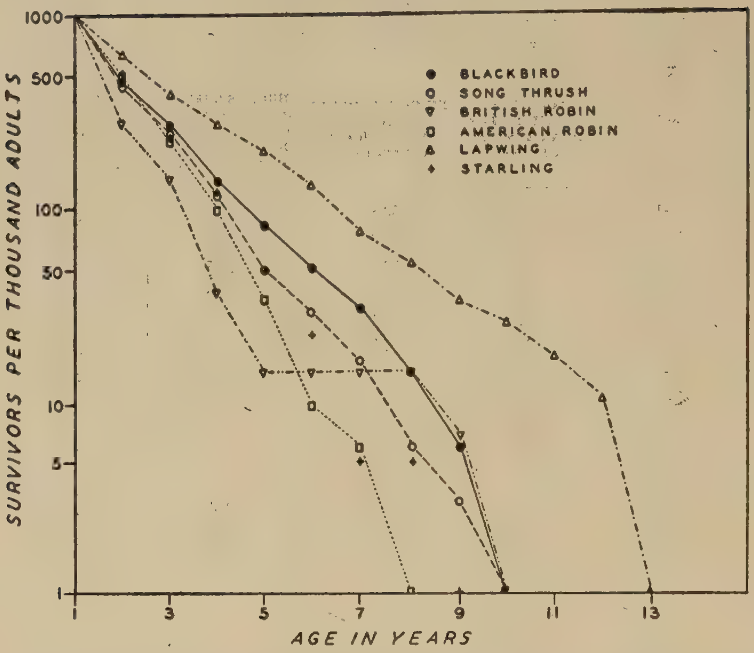

Fig. 3. Survivorship (l_x) Curves for the British Robin, Song Thrush, Blackbird, Starling, Lapwing and American Robin, Age being Expressed in Years

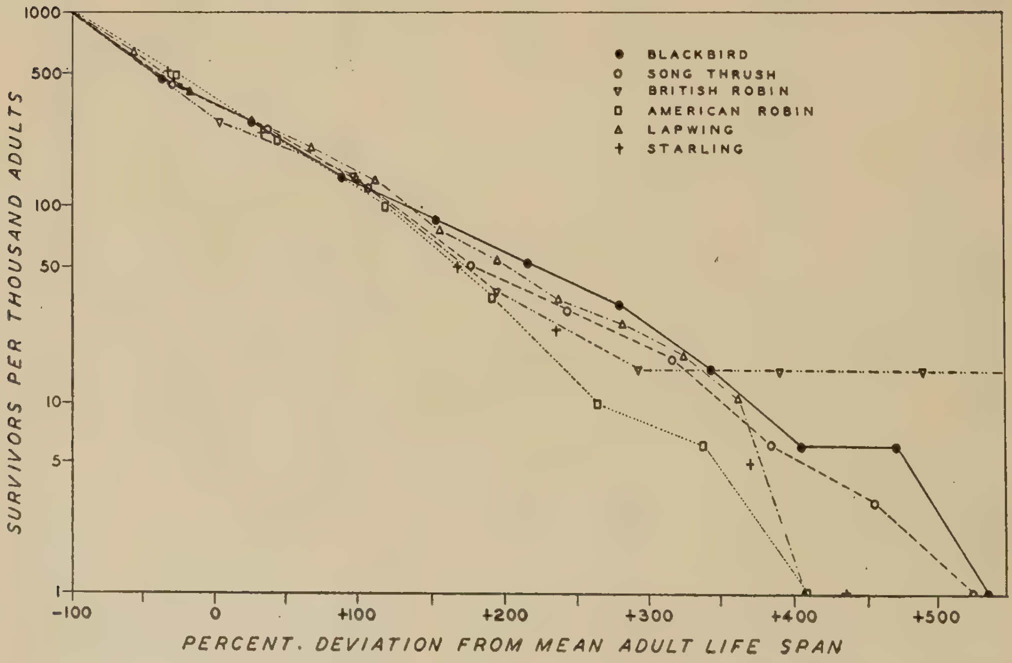

Fig. 4. Survivorship (l_x) Curves for the Same Species as in Fig. 3, Age being Expressed as Percentage Deviation from the Mean Length of Life

within the breeding range of the type subspecies between 1920 and 1940, and subsequently recovered dead. Farner's method of treatment of the data is analogous to Lack's, except that November 1 is taken as the starting point for the life table. The figures for the American robin have been entered in Table 5, and Figs. 3 and 4 indicate that this species suffers a mortality which is not only uniform with respect to age but is approximately the same as that of the British birds with respect to units of the mean life span.

Lack (1946) has recently discussed anew the question whether the disproportionately high mortality found among birds in their first year of life is real, or is due to the greater likelihood of their being picked up near the banding station. Analysing the returns between August 1 and January 1 for the blackbird, the song-thrush, the starling, and the lapwing, he found that most of these returns were of first-year birds, but that the proportion of first-year birds is no higher among those found by the bander or found near the banding station than it is among those found at a distance. The annual mortality is greater for first-year birds than for older birds when the calculations begin on August 1, and it remains greater when November 1 is the starting date, but by January 1 the constant level of adult mortality is reached. Calculations of adult mortality should therefore start on January 1, but from a comparative point of view this adjustment is of minor importance. The "disproportionate" mortality in the first year, starting from August 1, is really very little greater than in later years; it is scarcely visible on a logarithmic plot of survivorship (Figs. 3 and 4). The significant differences between juvenile and adult mortality, which would give a marked initial dip on such a plot, have been left out of account altogether, and August 1 is not too early, but too late a starting point.

TABLE 5

Life table for the American Robin (Turdus m. migratorius), based on returns of 568 birds banded as nestlings and known to be alive on November 1 of their first year. Age reckoned from November 1. Mean length of life after November 1—1.37 years

From Farner (1945)

x	x'	d_x	l_x	$1000\,q_x$	e_x
AGE (*years*)	AGE AS % DEVIATION FROM MEAN LENGTH OF LIFE	NUMBER DYING IN AGE INTERVAL OUT OF 1000 ALIVE ON NOVEMBER 1	NUMBER SURVIVING AT BEGINNING OF AGE INTERVAL OUT OF 1000 ALIVE ON NOVEMBER 1	MORTALITY RATE PER THOUSAND ALIVE AT BEGINNING OF AGE INTERVAL	EXPECTATION OF LIFE, OR MEAN LIFE TIME REMAINING TO THOSE ATTAINING AGE INTERVAL (*years*)
0–1	−100	503	1000	503	1.38
1–2	−27	268	497	539	1.26
2–3	+46	130	229	567	1.16
3–4	+119	63	99	636	1.03
4–5	+192	26	36	722	0.94
5–6	+265	4	10	400	1.10
6–7	+338	5	6	1000	0.50

Additional information on the lapwing is given by Kraak, Rinkel, and Hoogerheide (1940), who studied the age at death of 1333 continental birds banded as juveniles. The life table is not published, but the survivorship curve is reproduced, and is shown to be closely fitted by a line corresponding to a constant mortality rate of 40 per cent per year, reckoned from the first January 1 of life. This value is slightly higher than that found by Lack for the British population, but as the mean length of life is slightly lower, the mortality per unit of life span is the same.

It may be mentioned that the mortality rates for adult song sparrows, dealt with in the next section because the original data give l_x and not d_x, are fully consistent with the picture given by Fig. 4. The same may be said of Paynter's herring gull data, which have been presented separately because juvenile mortality is not specifically excluded, as it is for the other birds. All natural populations of birds so far investigated in any detail appear, therefore, to be alike in suffering a constant annual risk of death from early adult life to the end of the life span, this mortality being constant for birds at about 320 per thousand per hundred centiles of life span. Little is known of the seasonal distribution of these deaths, and it will be very interesting to discover whether non-migratory tropical birds suffer death in similar fashion.

Survivorship Directly Observed

The cases now to be discussed differ from the preceding in the character of the original observations. Instead of a fairly large sample of individuals about which little or nothing can be told except their age at death, we have a group of individuals known to have been born at a particular time and to have been present or absent at some later time. Their presence gives their survivorship, their absence implies death in the interval since they were last observed. This is the best sort of information to have, since it does not require the assumption that the age composition of the population is stable in time. Provided only that the season of birth is a small fraction of the age interval between successive observations, so that births can be assumed to be simultaneous, as in a *Drosophila* bottle, a horizontal life table can be directly constructed from the survivorship data. Unfortunately, most of the species which have been studied in this way have short spans of natural life, and when census data are obtained only once a year the number of points on the survivorship curve is too small to be satisfactory.

The best example of such observed survivorship comes from Hatton's work (1938) with the barnacle, *Balanus balanoides*. This work will be examined in great detail in a later section, and it is here necessary to say only that the case is very nearly ideal. The barnacle settles on rocks during a short time (two to six weeks) in early spring. Test areas were scraped clean one winter, and after new populations had settled, the survival of their members was followed at intervals of one to four months for three years. Barnacles which disappeared from the areas between observations were certainly dead, for emigration does not complicate the problem. Immigration, however, does present

TABLE 6

Life table for a typical population of Balanus balanoides, based on the observed survival of adult barnacles settling on a cleaned rock surface in the spring of 1930. The population is that at Cité, (St. Malo, France), a moderately sheltered location, at Level III, at half-tide level. The initial settling density (2200 per 100 cm²) is taken as the maximum density attained on May 15. Mean length of life 12.1 months

Data from Hatton (1938)

x	x'	d_x	l_x	$1000\ q_x$	e_x
*AGE (*months*)	*AGE AS % DEVIATION FROM MEAN LENGTH OF LIFE	NUMBER DYING IN AGE INTERVAL OF 1000 ATTACHING	NUMBER SURVIVING TO BEGINNING OF AGE INTERVAL OUT OF 1000 ATTACHING	MORTALITY RATE PER THOUSAND ALIVE AT BEGINNING OF AGE INTERVAL	EXPECTATION OF FURTHER LIFE (*months*)
0–2	−100	90	1000	90	12.1
2–4	−83.5	100	910	110	11.3
4–6	−67.0	50	810	62	10.5
6–8	−50.4	60	760	79	9.1
8–10	−33.9	80	700	114	7.8
10–12	−17.4	160	620	258	6.7
12–14	−0.9	80	460	174	6.7
14–16	+16.0	100	380	263	5.9
16–18	+32.2	50	280	179	5.7
18–20	+49.0	40	230	174	4.7
20–22	+65.4	100	190	526	2.4
22–24	+82.0	60	90	667	1.9
24–26	+98.8	20	30	667	1.8
26–28	+115.0	8	10	800	1.4
28–30	+132.0	2	2	1000	1.0

* Survivorship data given graphically by Hatton were smoothed by eye, and values at every other month were then read from the curve. The original observations were made at irregular intervals during three years.

difficulties, though since it is confined to the attachment seasons of subsequent years it should be possible to control it in subsequent work. There is one further disadvantage in that the life tables necessarily start at metamorphosis, leaving out of account mortality during pelagic larval stages. A life table for a typical population of barnacles is presented in Table 6.

The remaining examples suffer from more serious defects, and the data do not justify extended treatment. Green and Evans (1940) in their important study of the snowshoe rabbit (*Lepus americanus*) in Minnesota, followed the survival of marked individuals of several year classes, the total population present on the area and the number in each age-class being obtained by the mark-and-recapture method—also known as the "Lincoln index" (Jackson, 1939). Marking was done during most of the winter, and the annual census was made in February. It is perhaps unnecessary, and certainly uncharitable, to point out two sources of error in this excellent and ingenious work. In the first place, when marked individuals are released into a population and later recaptured, the calculation of the total population from the fraction

$$\frac{\text{size of sample when recapturing}}{\text{number recaptured}} \times \text{number marked}$$

depends on two assumptions, neither of which is likely to be true in this case: that there is no mortality between marking and recapturing; and that the marked individuals disperse at random through the whole population. Secondly, the flow of vital events in this population was so rapid, very few rabbits more than three years old ever having been found, that observations made annually can give only a very rough idea of the life table.

The latter objection applies with equal force to the study of a pheasant population made by Leopold et al. (1943) in Wisconsin. The former objection, though doubtless it could be urged, has less validity here, since the population, as ascertained by trapping, was checked by census drives.

Nice's thoroughgoing work (1937) on the song sparrow (*Melospiza melodia*) included a consideration of the survival of banded birds from year to year. The number of individuals which could be kept under continuous observation was necesarily small, and to find a sample large enough to use as the basis of a life table, it is necessary to take the 144 males banded in the breeding season between 1928 and 1935. Unfortunately, some of these males were of unknown age when first banded. Even if one assumes, (and the assumption is not far from the truth) that all new males appearing are first-year birds born elsewhere, the survival ratios from year to year will be too low if any adult males were still alive but failed to return to the area. Evidently such emigration is of minor importance with adult male song sparrows. With adult females, however, it is so serious that Nice did not think it worth while to publish the data on their return. Clearly, work on the survival of migratory birds is full of uncertainties, though the same may be said of resident species such as the wren-tit (Erickson, 1938) and the robin (Lack, 1943a).

All of these cases, snowshoe rabbit, pheasant, and song sparrow have one defect in common. This is the necessity of calculating the survival between birth and the first year of adult life from other data than those given by banding. For the snowshoe rabbit, the initial strength of the year-class is calculated from the estimated breeding population present and its known fertility. Leopold et al., lacking observations of their own on the pheasant mortality between birth and the first census period, used the estimates given by Errington for pheasants in another state. Nice calculates the survival of fledged young song sparrows to their first breeding season, by assuming a stable population and combining the estimated mean length of life of adults with their average nesting success. These procedures, while perfectly defensible as approaches to the problem, are inadequate substitutes for direct observation.

The three sets of data, with all their uncertainties, have been used as bases for synthetic life tables, and the survivorship curves are presented in Fig. 5. The snowshoe rabbit curve is that for the 1933 year class, the only one for which data are available on rabbits as old as four years. The juvenile mortality for 1933 is calculated by Green and Evans as 77 per cent between birth and the following February; for most other years it was higher, and for a few it was lower. Adult mortality, amounting to 70 per cent per year, was essentially constant throughout the study. The data for the pheasant are the average survival values for adults (30 per cent per year), combined with Errington's estimate of 84 per cent mortality between hatching and maturity. The song sparrow curve is calculated in two ways, the first including only the estimated mortality between fledging and the first breeding season (80 per cent) and the second also including the loss (40 per cent) between the laying of the eggs and fledging. The adult part of the life span is taken from the survival of the 144 males banded in 1928–1935.

The three curves show a pronounced diagonality from the adult stage onward. Initially, however, since the juvenile mortality in all cases is greater than the adult mortality, the curves show a dip which is most emphatic for the song sparrow reckoned from the egg, but which is invariably present. Here, then, we have for the first time survivorship curves which approach the positively skew rectangular type expected in theory from animals in nature. It is surprising that the approach is not closer, but it may well be true that the theoretical curve, in its most extreme form, is not to be looked for among terrestrial vertebrates.

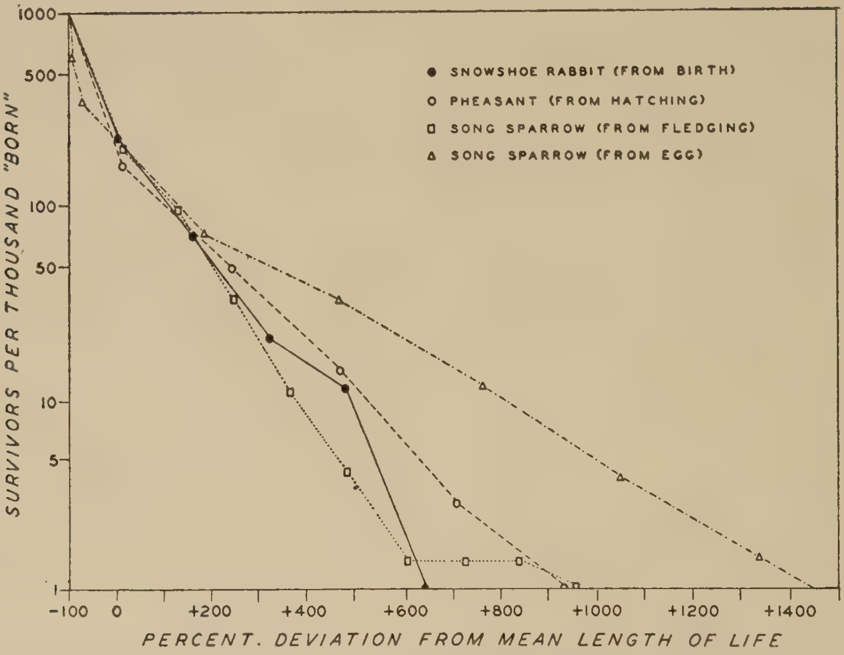

FIG. 5. SYNTHETIC SURVIVORSHIP (l_x) CURVES FOR THE SNOWSHOE RABBIT, THE PHEASANT, AND THE SONG SPARROW, THE LATTER CALCULATED FROM TWO DIFFERENT BIOLOGICAL AGES

Data for different parts of the life spans are derived in different ways, as explained in the text.

Age Structure Directly Observed

Ecological information of a third sort is available for a number of natural populations, principally of fishes and birds. In these cases the investigator has been able to determine how many individuals of each age are living in the population, and the age at death, though calculable from the shrinkage between successive age classes, has not been directly observed. This kind of information lends itself just as well as either of the others to the computation of life tables. As in the group where only the age at death is known, of course, it is necessary to assume the age composition to be unchanged with time. When this assumption is unreasonable, as it often is for fish populations, with their outrageous fluctuation in strength of year-classes, average age compositions obtained from several years' work can often be used. As it happens, however, all the life tables which fall in this third group are incomplete for one reason or another, and the data do not bear close comparison with such examples of natural life tables as those of the Dall sheep and the barnacle.

Kortlandt (1942) has recently given a very elaborate analysis of the Netherlands population of cormorants (*Phalacrocorax carbo sinensis*). Birds banded as nestlings were later observed in their breeding and playing colonies, the numbers on the bands being read with the aid of a telescope. The age distribution of the banded birds being known in 1940 and 1941, it should be possible to infer the age distribution of the total population and from this to compute the annual mortality suffered by each year-class. A number of complicating conditions are present in this case, however, making direct calculation unreliable and necessitating a more circuitous approach: (1) the size of the Dutch cormorant population is not constant, but has been increasing by about 10 per cent per year, as estimated by counts of nests at the breeding colonies; (2) differences between the observed sex ratio among sexually mature birds and the sex ratio predicted on the basis of estimated mortality by sex and age class show clearly that there is some *band mortality*; that is, some birds either lose bands or die because of the band, making estimates of natural mortality too high by a factor of about 2; (3) it is not possible to infer the complete age structure from observations made at breeding colonies, since the one- and two-year-old birds occupy "colonies" elsewhere, returning to their birthplaces to breed no sooner than their third year.

In view of these difficulties, and others which need not be discussed here, Kortlandt's results must be regarded as schematic and preliminary only, and scarcely warrant the construction of a life table. His computations suggest that cormorants suffer mortality somewhat as follows: 17 per cent between fledging and the first May 1; 8 per cent in the first year; 6 per cent in the second year; and about 4 per cent per year in the third to twelfth years. These are astonishingly low figures for a natural population, but it must be remembered that the population is increasing rapidly. It is interesting to find that the slight differential death rate between the sexes from the third year onward appears to favor the female rather than the male sex. It is not known whether this is true of birds generally, in contrast to most other animals (Geiser, 1923, 1924). MacArthur and Baillie (1932) have maintained that there is no evidence that differential mortality is correlated with the sex-determining chromosome mechanism, and that among moths and birds the male longevity is generally lower in conformity with the "rate of living" theory.

Huge numbers of returns of the common tern (*Sterna hirundo*) have been obtained at the Austin Ornithological Research Station on Cape Cod (Austin, 1942), where terns have been banded for over twenty years. Unfortunately the data are inadequately published, and in any case can yield only an incomplete life table, since terns, like other sea birds, scatter widely after birth and do not return to their birthplace until breeding age. Inspection of Austin's table, in which all returns are given by ages for the four years 1938–1941, suggests that the annual mortality is not constant from the fourth year onward, but varies from 178 to 636 per thousand even between the fourth and eighth years, when the numbers are large. It is not clear, however, whether or not the tern population has remained statistically constant during the period of study, i.e., whether the table really reflects the true natural mortality of an average or of any one year-class.

The literature of fisheries biology is full of attempts to estimate the mortality of fishes, to distinguish natural mortality from rate of exploitation, and to determine the rate of exploitation which, given certain mortality rates and certain relationships between age and size, will steadily yield an optimum catch. These complex questions are fully discussed in the important works of Russell (1942), Thompson and Bell (1934), and Ricker (1940, 1944), and by various authors in the *Rapports et Procès-Verbaux of the International Council for the Study of the Sea*, Volume 110, 1939. Little of this information can be directly used for our purpose. The explanation is as simple as it is regrettable: although the age of a caught fish can be ascertained with more or less complete confidence, fishes of all ages can not be caught with equal facility. Inevitably the methods so skilfully developed for catching fish of desirable sizes will fail to catch fish of undesirable sizes. It is true that on various occasions the whole fish population of a lake has been removed by poisoning or drainage. The estimates given by Eschmeyer (1939) for the abundance of large-mouth black bass (*Huro salmoides*) in Howe Lake, Michigan, at the time of its poisoning in 1937, may be cited as an example:

Age	*Number*
0	18,374
0 (cannibals)	229
I	25
II	10
III	105
IV	7
V and older	9
Total	18,759

The implication of enormously greater mortality in the first year of life is plain from these figures, but such data can not be taken as they stand, partly because of very variable annual recruitment, and partly because young of the year were removed from the lake at various times for hatchery purposes.

Lacking satisfactory observations of the complete age structure of the population, and faced with the obstacle of variable yearly recruitment in its most massive form, it is not surprising that fisheries workers have not attempted the construction of life tables, and have so far been content with the estimation of natural mortality among fishes of certain sizes only. This mortality is generally assumed to be constant with respect to age, and it may well be so for middle-aged fishes exposed to fishing; but a life table constructed from the available observations would certainly be lacking both head and tail.

As an example of the kind of information yielded by fisheries statistics, and of the methods used in their analysis, we may first take the data given by Ricker (1945) for the bluegill sunfish (*Lepomis macrochirus*) in Muskellunge Lake, Indiana. This is an especially instructive case, for it shows that despite great technical advantages not enjoyed by students of marine fisheries (a small, isolated, self-contained population; size and character of catch known with certainty by the investigator; age structure of the population checked by tagging methods), the difficulties remaining are still embarrassing.

Ricker first determined the rate of exploitation and the total mortality between one year and the next by what he called (rather inappropriately) the "direct" method, involving marked fish. In 1942, of 140 fish 145 mm. and larger (mostly 3 years old and older) marked prior to the opening of the season, 25 were recaptured by fishermen during the season, giving a rate of exploitation of 18 per cent. Estimated autumn fishing raises this figure to 19 per cent. Of 230 blue-gills 125 mm. and larger, marked prior to the 1942 season, 14 were recaptured in 1943. The rate of exploitation of fish in the same size group (then 155 mm. and larger) in 1943 was 15.1 per cent. It is necessary to calculate the number of 1942-marked fish present at the beginning of the 1943 season; this number is given by dividing the number recaptured in 1943 by the rate of exploitation in 1943, or $\frac{14}{0.151} = 93$. These 93 fish were the survivors of 230 marked fish present before the 1942 season, so the rate of mortality from one season to the next was $\frac{230 - 93}{230} =$ 60 per cent. Subtracting the 19 per cent rate of exploitation leaves 41 per cent as the natural mortality.

Ricker's "indirect" method is the life-table method in a crude form. A collection of scales from 529 blue-gills caught by fishermen in 1942 gave the following as the age structure of the sample:

Age.	I	II	III	IV	V	VI	VII	VIII
Number. . .	1	293	151	54	20	7	2	1

The age I fish was presumably caught by accident, and those of age II were not equally vulnerable to fishing during the first part of the season. From age III onward the age structure may be used to yield an estimate of the age-specific mortality rates (assuming uniform recruitment and mortality rates from year to year). These mortality rates in early ages, where the data are more reliable, are nearly constant at about 65 per cent. A weighted geometric mean by Jackson's method gives

$$\frac{1 + 2 + 7 + 20 + 54}{2 + 7 + 20 + 54 + 151} = 36\% \text{ survival}$$

$$= 64\% \text{ mortality.}$$

This is close to the 60 per cent mortality calculated by the "direct" method. However, both methods contain unproved and rather unlikely assumptions, and the agreement merely shows the order of magnitude of the total annual mortality. Moreover, the natural mortality as calculated so far is too low, as some of the fish caught by anglers would have died anyway. By making the additional assumption that the natural mortality is synchronized with the fishing mortality, Ricker calculates the former to be of the order of 50 per cent per year for blue-gills age III and older in four Indiana lakes. This is an important result, and one which will doubtless surprise many fisheries supervisors. It is not sufficient as the basis for a life table, however, since it does not include the mortality from birth to the third year of life, and since the method of weighting underrates the age-specific mortality at advanced ages. Ricker, in fact, thinks it not unlikely that the older fish are subject to a still higher mortality, but his data give no clear answer to the question.

It is a generally accepted conclusion that *adult* fishes, from the time they enter a fishery to the age at which they cease to be caught in significant numbers, suffer a more or less constant mortality with respect to age. Thus for these intermediate ages the survivorship curves, whether constructed vertically for a series of year-classes in any one fishing season, or horizontally for particular year-classes followed through several seasons, tend to fall on straight lines when plotted logarithmically. Such straight lines, with slopes changing according to the rate of exploitation, are implicit in Raitt's treatment of the statistics on the haddock (1939) and are conspicuous in Jensen's review (1939) of data on the cod, haddock, plaice, and herring in the North Sea. Whether the natural mortality, as distinguished from the fishing mortality, also is constant at all adult ages is an open question, but most fisheries workers would probably be prepared to assume that this is the case, in the absence of evidence to the contrary.

Direct observations of *juvenile* mortality in fishes are not easy to make, but a mass of indirect evidence points to the conclusion that it must be very much greater than adult mortality in many species. Some idea of this mortality can be had from Sette's work (1943) on the mackerel. Eggs and larvae of this pelagic species were caught on several systematically conducted cruises over the continental shelf between Martha's Vineyard and the Chesapeake Capes. Several broods spawned at short intervals during the season of 1932 were recognizable at later times and at geographically remote stations as separate modes in the frequency distributions of size and age. Assuming that the technique of plankton sampling gives a reliable estimate of the abundance of eggs and larvae of particular stages in the sea, their reduction in numbers gives a measure of their mortality. Sette's calculations show that the mortality is very great, and is substantially the same per unit time at all egg and larval stages. There is a noticeable rise in mortality rate, from about 10 to 14 per cent per day up to about 30 to 45 per cent per day, at the transition from larval to post-larval stages, when the fins are developing rapidly, but it falls again to the original level. The total mortality from the beginning of development to the 50 mm. stage, when the baby fish school like the adults and seek out their nursery grounds, is 99.9996 per cent. This fantastically high figure refers to a time interval of about *70 days*, and may be compared with values of 50 to 90 per cent *per year* estimated as the total mortality suffered by several species of commercial fishes as adults. Clearly, Pearl was correct in supposing that the survivorship curve for pelagic fishes may be of the J-shaped or positively skew rectangular form.

Though it can not be doubted that survivorship curves for fishes in nature will in general have an initial dip, it would be incorrect to conclude that this dip is invariably as pronounced as in the case of the mackerel. Barnaby (1944), for example, has considered the mortality of the Karluk River population of red salmon (*Oncorhynchus nerka*). Marking experiments suggest a total mortality in the ocean of about 79 per cent, while a calculation based on the reproductive potential yields a figure for the mortality in fresh water, between birth and seaward migration, of 99.55 per cent. The problem is complicated by the fact that the salmon may spend their lives in fresh water and in the ocean in various combinations of years, as 3 + 2 years, 3 + 3 years, 4 + 2 years, etc., so that these mortality rates refer to varying intervals of age. Thus there is no proof that the *annual* mortality rate is other than constant, and while no such deduction should be made from the data, it is evident that the age-specific mortality in fresh water can not be *very much* greater than in the ocean.

The data just presented have been grouped together because they give some conception of the form of the life table for certain species of fish, and the fact has been ignored that some of the information is not based on the age structure of the population, but on other kinds of evidence. This section may logically be concluded with a brief reference to the data for the fin whale, in which, as recent investigations have shown, the age of the female can be determined from the number of old corpora lutea in the ovary. By this method Wheeler (1934) arrived at the following as the age structure, observed over five seasons, 1926–1931, of the catch of female fin whales in the Antarctic:

Age	*Number caught*
3–4 years	130
5–6 years	95
7–8 years	72
9–10 years	53
11–12 years	37
13–14 years	28
15–16 years	10
17–18 years	4
19–20 years	1
21–22 years	1

The data imply (subject to the usual qualifications) a biennial mortality of about 26 per cent, increasing beyond the 15th year to much higher values. The author considers that the increased rate of loss with age is not real, but is due to failure of the older whales to return from their winter quarters in the north. This belief may or may not be well founded, but one suspects it to be predicated on the idea that mortality, at least when it is primarily due to exploitation, is constant among animals with respect to age. Edser (to whom the statistical analysis is credited) assumed, for the purpose of a rough calculation of the necessary rate of replacement, that the mortality between birth and breeding age is also 26 per cent. The improbability of this assumption may be surmised by reference to the life table for the Dall sheep (Table 1). Edser's calculation has the great merit of yielding a minimal estimate of the alarming exploitation being conducted by the whaling industry in the Antarctic. More realistic assumptions would darken the picture even more. In any case the data can not yet be cast into a life table.

Miscellaneous Survivorship Data

By means of the mark-and-recapture method, Jackson (1936, 1939) has given an analysis of the population of a tsetse fly (*Glossina morsitans*) in Tanganyika. Jackson was chiefly interested in determining the size of the population and its fluctuations from season to season. The death of flies in the one-week intervals between marking and recapturing struck at the foundation of the method, which assumes no such mortality. But by taking a geometric average of the survival of marked flies in successive weeks, and extrapolating backward one week, the number theoretically recapturable on the date of marking was calculable. From this figure, the first term in a geometric survival series, the population could be directly calculated for each week during the year over which the study was conducted. But the flies were of unknown ages when first marked, being recognizable simply as adult males (plus a few females) having had their first meal. Evidently the operation was designed to smooth out of existence those systematic changes in age-specific mortality in which we are interested here. A few males were marked *before* their first meal, and the returns of these should permit the construction of a life table beginning at early adult life, but the data are not published separately, and in any case are probably inadequate statistically.

Two other points of interest are raised by this resourceful study. The first deals with the sex ratio in the wild population. Data on the return of marked females are not numerous, but so far as they go they suggest a considerably lower mortality than among males, the calculated survival ratio being 0.716 for females and ranging from 0.307 to 0.622 (depending on the season) for males. Expressed as mortality rates, these values are equal to 284, and between 693 and 378 per thousand flies per week, respectively. As a result, the normal sex ratio among the wild flies must vary from 1.5 to 2.0 in favor of females. Yet the sex ratio at emergence from the pupa is unity. There is no evidence that emigration, though always a complicating factor, is performed differentially by the two sexes, and it is not improbable that here also, as in man and in so many other animals studied in the laboratory, the female is significantly more long-lived than the male. The oldest fly captured lived 13½ weeks after marking, and was a female.

The second point is that Jackson used two methods for the calculation of *a*, the initial term in a survivorship series. "Instead of considering the survival curve of flies marked in any one week and recaptured in subsequent weeks . . . we can equally well consider the recaptures of flies marked in previous weeks and recaptured in any one week. Subject to sampling errors, both methods should give the same value of *a*." The difference between the latter "negative" method and the former "positive" method is essentially the difference between a vertical and a horizontal life table. The two methods, while equally applicable to a series of mortality rates assumed to be constant and equal to the geometric mean, as in this case, will give different results for animals of known ages if the age-specific mortality rates change with time. Inasmuch as the smoothed mortality rates for flies of all ages in the population appear to change regularly with the season, being greater in the dry season, real life tables constructed for similar populations would have to be distinguished with care.

An elaborate program of trapping and marking has been carried out with a population of long-tailed field mice (*Apodemus sylvaticus*) by Hacker and Pearson (1946). This sort of work is full of pitfalls, arising mainly from the fact that the traps are attractive to the mice and tend to drain them from distances which are frequently too great to be safely negotiated a second time. As the mice were of unknown ages when first marked, the results need not be summarized in any detail here, but some of the conclusions are of interest in giving an indication of the form of the field mouse life table in nature.

The "standard" survival ratio for mature mice, as determined from repeated recaptures between December 1938 and April 1939, was 0.879, i.e., the mortality was 121 per thousand per month. But returns of these same mice in December and in March of the following year were much lower than expected from this ratio, implying that the mortality rate increases with age. Data for other years also show that the survival of the winter population is lower in the summer. Moreover, a study of returns of small, middle-sized, and large mice over three winter periods shows that the rates of loss are higher at both ends of the size distribution. Such scanty information can not be cast into a life table, but it is noticeable that a survivorship curve with two inflections fits well with that of the vole (*Microtus agrestis*), as established in the laboratory by Leslie and Ranson (1940).

Survival of Barnacles

Some of the advantages of the life table notation will now be illustrated by an analysis of the survivorship of the barnacle *Balanus balanoides*, as studied at St. Malo by Hatton (1938). The technical advantages presented by intertidal barnacles as objects of population research have been discussed in an earlier section, and a typical example of a barnacle life table has been given in Table 6. The relevant information about the biology of the species, as elucidated by Runnström (1925), Moore (1934), and Hatton, may be briefly summarized:

Balanus balanoides is a typical intertidal species, occurring primarily within the mean range of neap tides, where it often makes dense incrustations on all solid objects. It breeds in the fall, the nauplii being held in the mantle cavity for some time before liberation, while attachment and metamorphosis of the cyprid larvae takes place in the early spring, the exact time doubtless depending on the temperature. The attachment season lasts about six weeks. The intensity of attachment varies with the exposure to surf and the tidal level, being greatest at most exposed localities and at lower levels. The growth rate after attachment is greatest at lower tidal levels in the first year of life, but in subsequent years the growth at higher levels surpasses that at lower levels. Mortality, however, is also greater at lower levels, as shown by survival of barnacles of known ages from year to year, and thus the few barnacles at high levels (up to the mean level of high-water neap tides) are larger after a year's growth and live longer than those lower down. The maximum longevity appears to be about 5 years, but is much less at lower levels.

It is not clear which of these facts are simple responses to the physical ecology of the intertidal zone, and which are biotic effects. It is easy to suppose that the growth rate might be best at lower levels, where the barnacles are more continuously submerged and therefore take food more frequently. It is not so easy to explain the decline of growth rate with age at these levels (or the increase of growth rate with age at higher levels), unless it is in some way related to the population density; yet the growth differences are said to be observable in the absence of crowding. The low attachment densities at high levels presumably reflect the time necessary for a cyprid to attach, for the time available on any one tide decreases with the height. But after attachment the higher levels are exposed for longer periods to desiccation, direct sunlight, and rainwater, and the enhanced survival under these conditions is difficult to understand except as a function of the low population density.

The relation between population density and longevity is well known for certain laboratory animals. In general the length of life is curtailed by overcrowding (Pearl, 1946; Davis, 1945). In certain well-studied cases, however, the mean length of life has been found to increase at densities above the minimum, to decrease at very high densities, and to be greatest at some intermediate density (Pearl, Miner, and Parker, 1927). Pratt's proof of an optimum density for longevity of *Daphnia magna* (1943) is particularly convincing, since the densities were actually maintained constant throughout the life of the animals, and were not permitted to decrease with the gradual extinction of the initial cohort.

It is of considerable importance, therefore, to examine Hatton's data, which fortunately are published in full, for evidence of the relationship between longevity and population density in *Balanus balanoides*. Hatton studied nine different populations, allowed to settle on cleaned areas in 1930, and followed for three years. Three different levels were chosen at each of three localities as follows:

Localities	*Levels*
Décollé Ouest, exposed	II—mean high-water neap tide
Décollé Est, sheltered	III—half-tide
Cité, moderately sheltered	IV—mean low-water neap tide

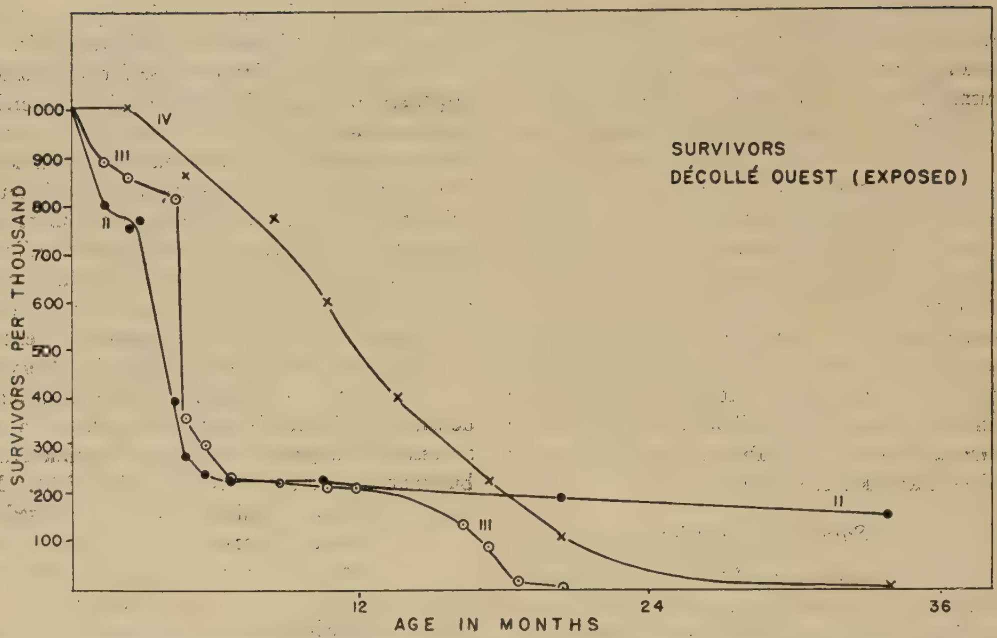

FIG. 6. SURVIVORSHIP (l_x) CURVES FOR THREE OF THE NINE POPULATIONS OF BALANUS BALANOIDES STUDIED AT ST. MALO BY HATTON (1938)

The locality, Décollé Ouest, is exposed to surf. The initial density of attachment, taken as the maximum density attained on May 15, 1930, was as follows: II (at mean high-water neap tide level), 790 per 100 cm²; III (at half-tide level), 2330 per 100 cm²; IV (at mean low-water neap tide level), 1500 per 100 cm².

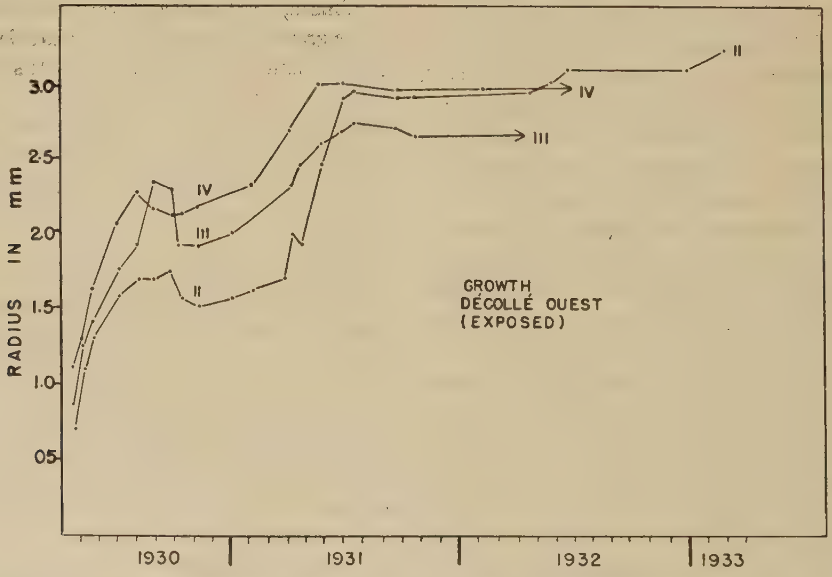

FIG. 7. GROWTH CURVES FOR BARNACLES CORRESPONDING TO THE THREE POPULATIONS OF FIG. 6, BUT OBTAINED FROM UNCROWDED SPECIMENS

The measurements began on April 1, 1930, and the points plotted are the average lengths (at the base, in the rostro-carinal axis), divided by 2. Each point represents an average of about 50 measurements.

Survivorship curves for the three populations at Décollé Ouest, converted to a relative (per thousand) basis, are shown by way of illustration in Fig. 6. It may be seen that the only population having surviving members after three years was that at Level II, where the initial population density was also least. The same relationship between density and survival was observed at the other two localities. But the matter is not so simple as it looks, for the growth rates must be taken into account in evaluating the degree of crowding on the areas. The corresponding growth curves for the Décollé Ouest populations are shown in Fig. 7. The measurements were made, not on the original populations, but on barnacles from adjacent cleaned areas, where the initial density was not allowed to exceed 100 per square decimeter, so that the growth was uninfluenced by crowding. The measurements given are the average lengths (in the rostro-carinal axis) of 50 individuals. This explains the curious fact that the sizes decrease during the winter: negative growth is biologically impossible in this case, and evidently there was a relatively great loss of older barnacles each winter. For purposes of calculation the radius of a barnacle has been taken to equal half the length, and the reasonable growth figures (ignoring negative increments) have been fitted to equations of the form

$$r = at^b$$

where r is the radius and t is the time in months.

Hatton's survivorship curves give the population per unit area at any time. The area at the base of an average uncrowded member of the population at any time can be calculated from the growth curve on the assumption, which is sufficiently accurate for the purpose, that the barnacles grow as expanding circles. The degree of crowding attained at any time can be evaluated as follows: (Grateful acknowledgment is due to Dr. John Ferry, of the University of Wisconsin, for the elegant following formulation.)

If barnacles of radius r settle at random within distance D of each other, and grow as expanding circles, so that at any time the radii r are equal, any barnacle which settles within distance $2r$ will be in contact with or overlap another. The number of binary contacts per barnacle will be given by:

$$\int_0^{2r} \frac{N}{A} \cdot 2\pi D \cdot dD$$

or, evaluating:

$$4\pi r^2 \frac{N}{A}$$

where $\frac{N}{A}$ is the density per unit area. The total number of binary contacts per unit area will be this expression times the density times $\frac{1}{2}$ (because each contact is counted twice):

$$C = 2\pi r^2 \left(\frac{N}{A}\right)^2$$

This value C, the *crowding coefficient*, can be evaluated in terms of contacts per square centimeter, and is a function of the density and of the radius of an individual barnacle.

The crowding coefficients for Hatton's nine populations are given for selected times in Table 7, together with the observed density and the average radius of a barnacle at the same times. The expectation of life of a barnacle at the time in question is calculated by ordinary life table methods. Plotting C against e_x gives the graph shown in Fig. 8.

Evidently the population density, when considered in this way, has a definite effect on the survival of *Balanus balanoides*. The effect is not linear, but becomes less marked at higher degrees of crowding. Evidently, too, the relationship between survivorship and crowding is less definite at advanced ages, for the points for 18 months diverge from the curve.

It seems fairly certain that this discrepancy is due to the fact that the treatment has ignored the new settlements of barnacles which were added to the populations in subsequent years. The new arrivals can be treated by an extension of Dr. Ferry's mathematical approach, but it becomes necessary to decide whether there is any superincrustation, i.e., whether the area exposed to settlement, A, is (1) the same as the original area, (2) equal to the unoccupied area, or (3) has some intermediate value. No decision can be reached on this point from Hatton's account, which moreover gives only the second-year settlements, without subsequent data on the survival of the 1931 year-class or any information on the 1932 year-class. The data, however, are suggestive in that all the populations which diverge widely at 18 months from the curve of Fig. 8 received high second-year settlements, while the "good" points are from populations which received relatively little recruitment in 1931. Since in general the populations with highest initial densities will receive the most considerable reinforcement in subsequent such as the one drawn in Fig. 8, is an illusion. But only further work will permit a deeper analysis of this exceptionally interesting case.

TABLE 7

Population density, calculated radius, crowding coefficients, and expectation of life at selected times for nine populations of Balanus balanoides at St. Malo

Original data from Hatton (1938)

POPULATION (*Locality and Level*)	t TIME (*months*)*	N/A DENSITY PER CM^2	r RADIUS (*mm.*)	C CROWDING COEFFICIENT: *contacts per cm*^{2} = $2\pi r^2(N/A)^2$	e_x EXPECTATION OF FURTHER LIFE (*months*)†
Décollé Est II	0	4.0	1.08	1.17	23.1
	6	2.4	1.65	0.98	29.6
	12	2.1	1.92	1.02	27.2
	18	1.9	2.11	1.01	23.7
	24	1.5	2.27	0.73	23.1
	30	1.5	2.39	0.81	17.7
Décollé Est III	0	11.9	1.12	11.24	13.8
	6	8.3	1.59	10.87	12.8
	12	5.4	1.80	5.92	12.6
	18	4.2	1.94	4.09	9.1
	24	2.0	2.06	1.07	9.9
	30	1.0	2.16	0.29	12.2
Décollé Est IV	0	15.0	1.41	27.91	9.5
	6	8.4	1.80	14.35	7.5
	12	4.8	1.97	5.61	4.9
	18	1.8	2.08	0.88	1.2
Décollé Ouest II	0	7.9	1.34	7.07	11.0
	6	1.9	1.82	0.75	31.2
	12	1.7	2.03	0.75	28.5
	18	1.5	2.18	0.67	24.5
	24	1.4	2.29	0.65	20.3
	30	1.3	2.38	0.61	15.8
Décollé Ouest III	0	23.3	1.50	76.28	7.0
	6	6.3	1.94	9.34	8.7
	12	4.9	2.12	6.81	4.7
	18	1.2	2.25	0.46	1.0
Décollé Ouest IV	0	15.0	1.74	42.55	12.6
	6	12.6	2.20	48.41	8.2
	12	7.3	2.40	19.35	5.6
	18	3.0	2.54	3.65	3.7
	24	0.6	2.64	0.16	2.9
	30	0.08	2.73	0.03	2.0
Cité II	0	10.0	1.24	9.61	14.3
	6	3.4	1.67	2.03	28.6
	12	2.9	1.89	1.88	27.2
	18	2.8	2.00	1.97	22.5
	24	2.5	2.10	1.73	19.0
	30	2.2	2.19	1.45	15.2
Cité III‡	0	22.0	1.32	53.22	12.1
	6	16.7	1.66	48.05	9.1
	12	10.1	1.80	20.70	6.7
	18	5.1	1.89	5.85	4.7
	24	0.7	1.96	0.11	1.8
Cité IV	0	23.8	1.44	74.10	11.2
	6	12.9	1.71	30.68	12.2
	12	11.0	1.82	25.29	7.9
	18	6.1	1.90	8.41	5.4
	24	2.6	1.95	1.62	2.5

* These are the times corresponding to the density figures (read from the survivorship curves), beginning at 0 = 15 May. The growth curves begin on 1 April, and the time values for radius as stated are actually 1.5, 7.5, 13.5, 19.5, 25.5, and 31.5 months.

† Computed on the assumption that those populations still having surviving members after 3 years would have terminated at 5 years.

‡ Life table for this population given in Table 6.

years, it is easy to imagine that over the years the effect of unit change of crowding on survival, $\frac{de_x}{dC}$, will be greatest for these populations. This argument carries the implication that a single curve,

Returning to the original question, whether there is a density above the minimum which is optimal for the longevity of *Balanus balanoides* in nature, Fig. 8 indicates that there is not. The expectation of life is greatest when the crowding coefficient is least, and the curve does not rise before it falls. This negative evidence is probably not conclusive, and a larger body of data, preferably obtained under conditions which are less variable as regards factors other than crowding, might give a different answer. But there is no particular reason to expect that a species such as this one would benefit greatly from mutual support. It is possible to point to another barnacle in which the case may be otherwise. This is *Chthamalus stellatus*, which flourishes best at an intertidal level above that of *B. balanoides*. Here it is exposed to sun and drought for long periods, and Monterosso (1930) has found that it is remarkably hardy, specimens having survived for three years on a laboratory table with only one or two days' immersion in sea water each month. Hatton suggests that the chances of survival of a young *Chthamalus* are improved if it settles in the shade of a larger individual; at any rate, the larvae tend to attach in the shade in greater numbers, when ridges of cement are built upon the rocks. Moreover, while attached and growing *B. balanoides* were frequently found to dislodge each other from the substratum, this phenomenon was never observed with *Chthamalus*.

Hatton's work included survival studies of *Chthamalus* as well as of *B. balanoides*, but as the longevity of the former is greater (see also Moore and Kitching, 1939), few of the populations had run their courses when the experiments were terminated at the end of three years. As a result, the expectation of life cannot be calculated with any confidence. Annual mortality rates for six populations (three at Level I, above the *B. balanoids* zone; and three at Level II, where densities of *B. balanoides* were low) are arranged in Table 8 for direct comparison with the density. The table shows that the populations having very low densities suffered higher mortality rates on the average than those below the dashed line in the table, which had higher densities. The difference is more pronounced when the first year's mortality is omitted, but in neither case is the difference significant statistically. The predicted relation between density and survivorship of *Chthamalus* is therefore not proven, and the question remains open.

Mention has been made in an earlier section of a

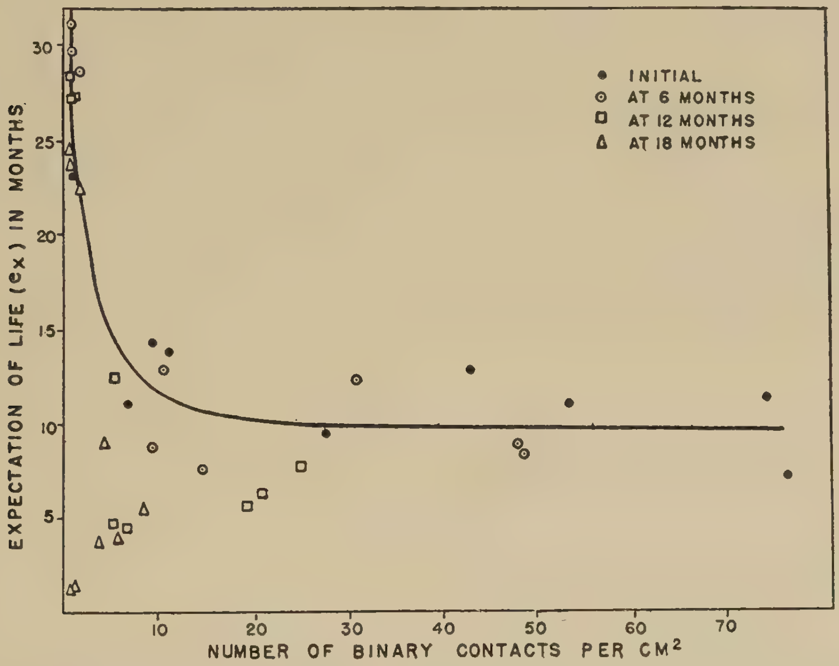

FIG. 8. RELATION BETWEEN EXPECTATION OF LIFE (e_x) OF BALANUS BALANOIDES AT SELECTED TIMES AND THE CROWDING COEFFICIENT (CONTACTS PER SQUARE CENTIMETER) AT THE SAME TIME
Data in Table 7, calculated from data of Hatton.

defect inherent in the life tables calculated from experiments like Hatton's, in that the observations start with metamorphosis, and the pelagic larval life is neglected. Some idea of the mortality during the earliest attachment stage, the interval between attachment of the cyprid and its transformation to an adult barnacle, can be gained from the unpublished studies of Weiss at Miami Beach, Florida.

TABLE 8

Annual mortality of Chthamalus stellatus at St. Malo in relation to population density
Data from Hatton (1938), Tables XXXVI–XXXVIII

POPULATION (LOCALITY AND LEVEL)	FIRST YEAR		SECOND YEAR		THIRD YEAR	
	Initial density per 100 cm²	Mortality %	Density per 100 cm²	Mortality %	Density per 100 cm²	Mortality %
Décollé Ouest I	21	4.8	20	10.0	18	16.6
Décollé Est II	39	10.3	35	20.0	28	28.6
Cité I	44	9.1	40	17.5	33	9.1
Décollé Est I	48	31.2	33	9.1	30	36.7
Cité II	184	11.4	163	13.5	141	8.5
Décollé Ouest II	270	17.4	223	11.2	198	14.1

Permission to present these results in advance of publication has been courteously granted by Mr. C. M. Weiss of the Woods Hole Oceanographic Institution.

Weiss observed the daily attachment of cyprid larvae (mainly *Balanus improvisus*) to glass slides exposed each twenty-four hours for more than three years. At the same time, records were kept of the attachment of adult barnacles to glass panels exposed each month at the same locality. The time required for a cyprid to grow into an adult barnacle large enough to be counted varies from one to two weeks according to the season. By summing the daily cyprid attachments over a two- to three-week period, therefore, and comparing the figures with the number of adult barnacles found on the panels at the end of the month, a measure of the survival between cyprid and adult stages was obtained. The results are shown in Fig. 9, the ratio of surviving barnacles to cyprids being plotted against the intensity of cyprid attachment. The curve shows clearly that a cyprid's chances of successful growth to maturity vary inversely with the density of attachment: when few cyprids attach most or all of them survive to become barnacles, but when cyprid densities are high the mortality is much greater, reaching 95 per cent (survival ratio 0.05) at the greatest densities observed.

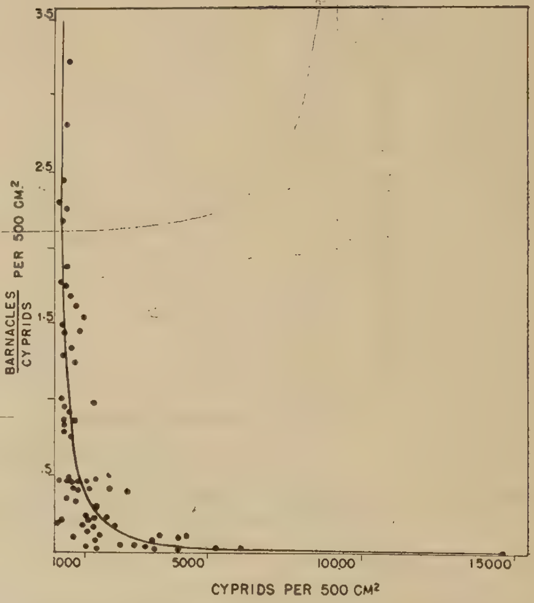

Fig. 9. Relation Between Survival of Barnacles to Maturity and the Intensity of Cyprid Attachment at Miami Beach, Florida

Cypris attachment was observed on glass slides exposed for twenty-four hours; the barnacles were counted on glass panels exposed for twenty-eight days. Daily cyprid attachment figures have been summed over two or three weeks, according to the season, for comparison with the number of surviving barnacles. From unpublished results of C. M. Weiss, Woods Hole Oceanographic Institution.

Inspection of the scale of barnacle:cyprid ratios in Fig. 9 brings out an apparent paradox in that ratios above 1.0 were frequently observed, i.e., in least, and the curve does not rise before it falls. This negative evidence is probably not conclusive, and a larger body of data, preferably obtained under conditions which are less variable as regards factors other than crowding, might give a different answer. But there is no particular reason to expect that a species such as this one would benefit greatly from mutual support. It is possible to point to another barnacle in which the case may be otherwise. This is *Chthamalus stellatus*, which flourishes best at an intertidal level above that of *B. balanoides.* Here it is exposed to sun and drought for long periods, and Monterosso (1930) has found that it is remarkably hardy, specimens having survived for three years on a laboratory table with only one or two days' immersion in sea water each month. Hatton suggests that the chances of survival of a young *Chthamalus* are improved if it settles in the shade of a larger individual; at any rate, the larvae tend to attach in the shade in greater numbers, when ridges of cement are built upon the rocks. Moreover, while attached and growing *B. balanoides* were frequently found to dislodge each other from the substratum, this phenomenon was never observed with *Chthamalus.*

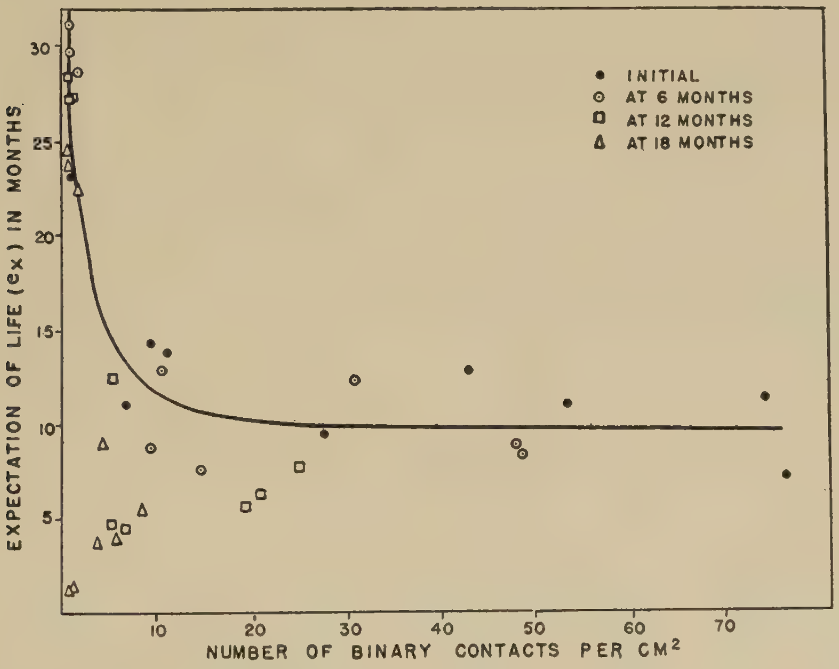

FIG. 8. RELATION BETWEEN EXPECTATION OF LIFE (e_x) OF BALANUS BALANOIDES AT SELECTED TIMES AND THE CROWDING COEFFICIENT (CONTACTS PER SQUARE CENTIMETER) AT THE SAME TIME
Data in Table 7, calculated from data of Hatton.

Hatton's work included survival studies of *Chthamalus* as well as of *B. balanoides*, but as the longevity of the former is greater (see also Moore and Kitching, 1939), few of the populations had run their courses when the experiments were terminated at the end of three years. As a result, the expectation of life cannot be calculated with any confidence. Annual mortality rates for six populations (three at Level I, above the *B. balanoids* zone; and three at Level II, where densities of *B. balanoides* were low) are arranged in Table 8 for direct comparison with the density. The table shows that the populations having very low densities suffered higher mortality rates on the average than those below the dashed line in the table, which had higher densities. The difference is more pronounced when the first year's mortality is omitted, but in neither case is the difference significant statistically. The predicted relation between density and survivorship of *Chthamalus* is therefore not proven, and the question remains open.

Mention has been made in an earlier section of a defect inherent in the life tables calculated from experiments like Hatton's, in that the observations start with metamorphosis, and the pelagic larval life is neglected. Some idea of the mortality during the earliest attachment stage, the interval between attachment of the cyprid and its transformation to an adult barnacle, can be gained from the unpublished studies of Weiss at Miami Beach, Florida.

Permission to present these results in advance of publication has been courteously granted by Mr. C. M. Weiss of the Woods Hole Oceanographic Institution.

Weiss observed the daily attachment of cyprid larvae (mainly *Balanus improvisus*) to glass slides exposed each twenty-four hours for more than three years. At the same time, records were kept of the attachment of adult barnacles to glass panels exposed each month at the same locality. The time required for a cyprid to grow into an adult barnacle large enough to be counted varies from one to two weeks according to the season. By summing the daily cyprid attachments over a two- to three-week period, therefore, and comparing the figures with the number of adult barnacles found on the panels at the end of the month, a measure of the survival between cyprid and adult stages was obtained. The results are shown in Fig. 9, the ratio of surviving barnacles to cyprids being plotted against the intensity of cyprid attachment. The curve shows clearly that a cyprid's chances of successful growth to maturity vary inversely with the density of attachment: when few cyprids attach most or all of them survive to become barnacles, but when cyprid densities are high the mortality is much greater, reaching 95 per cent (survival ratio 0.05) at the greatest densities observed.

TABLE 8

Annual mortality of Chthamalus stellatus at St. Malo in relation to population density
Data from Hatton (1938), Tables XXXVI–XXXVIII

POPULATION (LOCALITY AND LEVEL)	FIRST YEAR		SECOND YEAR		THIRD YEAR	
	Initial density per 100 cm²	Mortality %	Density per 100 cm²	Mortality %	Density per 100 cm²	Mortality %
Décollé Ouest I	21	4.8	20	10.0	18	16.6
Décollé Est II	39	10.3	35	20.0	28	28.6
Cité I	44	9.1	40	17.5	33	9.1
Décollé Est I	48	31.2	33	9.1	30	36.7
Cité II	184	11.4	163	13.5	141	8.5
Décollé Ouest II	270	17.4	223	11.2	198	14.1

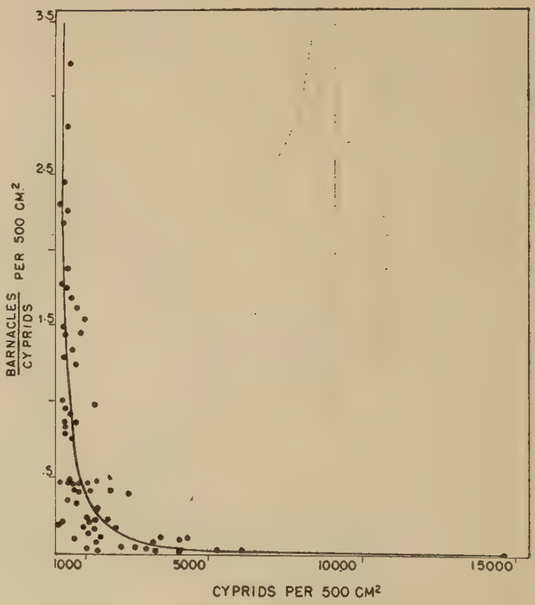

FIG. 9. RELATION BETWEEN SURVIVAL OF BARNACLES TO MATURITY AND THE INTENSITY OF CYPRID ATTACHMENT AT MIAMI BEACH, FLORIDA

Cypríd attachment was observed on glass slides exposed for twenty-four hours; the barnacles were counted on glass panels exposed for twenty-eight days. Daily cyprid attachment figures have been summed over two or three weeks, according to the season, for comparison with the number of surviving barnacles. From unpublished results of C. M. Weiss, Woods Hole Oceanographic Institution.

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Although it is abundantly clear that much of the mortality suffered by natural stands of barnacles is directly related to population density, much of it certainly is not. Predators, such as whelks and limpets, account for many deaths at all ages, and physical factors, including desiccation in summer and abrasion by boulders in winter, are also important. We are not yet able to dissect the barnacle life tables to expose the causes of death. It is enough for the purposes of this review to have pointed out: (1) the attraction of barnacle incrustations as objects for population research; and (2) the advantages of life table methods in their study.

COMPARISONS AND CONCLUSIONS

It is now apparent that, owing to the different ways in which data have been collected, all ecological life tables are not strictly comparable among themselves, and a summary graph containing survivorship curves for all the species considered would be misleading in the extreme. It is also true, though not so obvious, that within any one group of life tables, such as the "d_x observed" group or the "l_x observed" group, comparisons are also apt to lead us astray. For the various life tables so far constructed *take their origin at different biological ages*. Is it fair to compare a bird life table, beginning at early adult life, with the Dall sheep life table, which begins at birth, or with the life table of a sessile invertebrate, beginning at attachment or metamorphosis? Evidently not; birth itself is not an age of universal biological equivalence outside the placental mammals, and for a broader view of comparative mortality the only safe point of reference would be the fertilized ovum.

This reservation should perhaps not be applied too literally. Human and insect survivorship curves have been compared in the past, and the comparison is instructive, despite the very different origins and statistical foundations of the life tables. It is possible to compare the survivorship of an insect such as *Drosophila*, beginning at sexual maturity, with that of a laboratory population of black widow spiders (Deevey and Deevey, 1945) which enter their life table at the antepenultimate instar when the sexes become distinguishable. The comparison, which of course is purely qualitative, suggests that organisms are born at different points on their survivorship curves, so to speak, and that heavy juvenile mortality may be carried over into later life as a neotenic character. This is the statistical aspect of that ancient proverb which Cicero quotes disparagingly, "grow old early if you would be old long."

The cognate suggestion has been made that altricial and praecocial birds should be examined in the light of this hypothesis. Unfortunately, such a comparison cannot yet be made. We now have life tables of a sort for several altricial species, (song sparrow, Turdidae, etc.) and for at least one markedly praecocial bird (the pheasant), but the data are lacking for those early ages at which the comparison might have some meaning.

If bird life tables cannot even be compared with one another except from adult ages onward, we can hardly make very enlightening comparisons between birds and other animals. The ecological information is deficient, to a variable degree it is true, but still deficient, for the early ages; and this is the segment of the life curve on which future investigators must concentrate their efforts. The most that can be said at present is that the more nearly complete natural life tables (Dall sheep, barnacle, rotifer) give no ground for supposing that ecological life tables are invariably diagonal, as is so often assumed *faute de mieux* in fisheries work. Increases and decreases in mortality rate must be expected at any age, as the laboratory populations also show.

Related to the paucity of data near the beginning of life is the remarkable absence, among the examples adduced, of life curves approaching Pearl's "Type III" distribution. Only the synthetic survivorship curve for the song sparrow calculated from the egg stage (Fig. 5) shows the pronounced dip in early life associated with this form. But Sette's data for the mackerel show that pelagic fishes actually fall here; the barnacle and the rotifer might also fall here if their life tables were complete, and ecologists will await with interest the construction of a life table for the oyster.

It is pertinent to inquire whether the ecological life tables throw any light on the relation between the different theoretical types of survivorship curve (Fig. 1). It is a well known property of human longevity that while the mean age at death shows extreme variation among different populations, ancient and modern, and has shown a marked increase in Europe and the United States in recent decades, the maximum life span is fixed (Dublin and Lotka, 1935; Pearl, 1946). In other words, the human survivorship curve is like a rubber band, fixed at points corresponding to birth and about the 115th year, and while medical science has succeeded in stretching the band more and more toward the upper side of Fig. 1, the termini have remained fixed as they were in Roman times.

If the maximum life span is fixed for all species by physiological considerations, as it probably is, the mean life span is not. Lack (1943b) points out that a young blackbird in nature can expect to live for but 8 per cent of its potential life span, compared to some 60 per cent for a juvenile human. Evidently there is much room for improvement in the expectation of life of species in the wild, to judge from the known longevity of some of them in captivity. As has been shown, birds as a group seem to have remarkably diagonal survivorship curves, the mortality being constant for a given bird with respect to age, and for all birds so far studied with respect to units of mean life span. This means that experience of life is of no use to a bird in avoiding death, although Farner (1945) raises the question whether the apparent diagonality may not be a result of insufficient data.

The case is quite otherwise with the Dall sheep, with its low mortality during middle life. This species seems to have evolved a mechanism for stretching its mean life span toward the maximum. Whether this has come about because of intimate demographic contact with a single important predator or for some other reason is a "puzzling question." Such an enhancement of survival during the years of maximum reproductive efficiency has important implications for the whole population problem, including the question of the nature of internally generated cycles; but on this matter little more can be said than that the mathematical methods are available for a study of the relation between the fertility schedule and the death rate structure when the data come to hand (Leslie, 1945).

Bodenheimer (1938) has maintained that not only is the maximum life span fixed for a species, but that the potential mean longevity is the same as the maximum. On this view a species has a "physiological life table" of the negatively skew rectangular type, and a more diagonal or positively skew "ecological life table" which is the result of premature mortality. All such mortality is thus regarded as environmentally produced. This position is probably not tenable as a basis for a general theory of mortality, since there appears to be no reason why "endogenous senescence" (in Pearl's phrase) should be strictly confined to the end of the life span. Even in genetically homogeneous populations the members are not identical, and endogenous senescence must have a probability distribution which is not necessarily regular, though it may well be more so than that of "exogenous senescence." In any case, since we can not observe physiological survivorship except in an environment of some sort, Bodenheimer's conception would appear to be non-operational.

The question at issue resolves itself into the relation between the mean and the maximum life span. In theory there is a simple answer: the ratio of the maximum to the mean approaches 1.0 as a limit for Type I, approaches infinity for Type III, and its actual value for Type II depends on the level at which we permit the abscissa of Figure 1 to intersect the ordinate. If we decide to terminate the diagram when a cohort of 1000 individuals has been reduced to 1, a diagonal survivorship line will intersect the age axis at some point above 1.0, but if we start with 100,000 individuals the same line projected will give a higher maximum age for the last survivor. Reference to Figs. 2, 4, and 5 will make the matter plain, when it is realized that an age value of +100 per cent deviation from the mean corresponds to a maximum: mean ratio of 2.0, one of +500 per cent corresponds to a ratio of 6.0, etc. In all cases we have started with 1000 individuals, simply because the samples were of less than 1000 to begin with, and only three places at most can be significant. Had we larger samples available the maximum life span, as shown on the abscissas of Figs. 2, 4, and 5, would have been higher for a given mortality rate.

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It should now be clear that we cannot yet formulate the relationship exactly. One stumbling block is that with a cohort of 1000 individuals the 1 per thousand level has lost all semblance of reliability: taking Fig. 4 as an illustration, we might well find that the last hundred birds in a cohort of 100,000 really have gained some benefit from their accumulated experience of life, and die at decreasing rates. This would mean that the true survivorship curve is concave. It is equally possible that these hypothetical survivors of a larger cohort would be found to be decrepit, and to die at greatly accelerated rates, giving a convexity to the tail of the survivorship curve.

The other obstacle to an exact formulation is that the mean length of life is calculated from different starting points in the cases before us, so that an observed relation between maximum and mean has no quantitative significance as a basis of comparison between species. Empirically, it will eventually be possible to divide animals into three groups, somewhat as follows: those in which the maximum length of life is between two and six times the mean may be called "thrifty" (the Dall sheep, rotifer, and barnacle might fall here, along with most of the populations studied in the laboratory); those in which the ratio lies between 6.0 and 15.0 (as perhaps in song birds) might be called "indifferent"; those which on the average realize less than one-fifteenth of their maximum life span might be called "prodigal." These limits would have to be arbitrarily defined by the age (in units of mean life span) attained by the oldest individual in a cohort of 1000. But such limits can not yet be specified, and the values assigned are pure guesses, based on data which we know to be inadequate, and intended simply for illustration.

So far we have confined our attention almost exclusively to the *form* of the life table, and have said very little about the *causes* of death other than to imply that they are suitable subjects for ecological investigation. Authors who have discussed the matter in some detail for particular cases have not reached very satisfactory general conclusions. Thus Ricker (1945) decides that "senile death is an everyday occurrence among bluegills and crappies," and Lack (1943a) says, "Who killed cock robin is, for the most part, still a mystery." Errington (1945, 1946) has argued energetically against the generally accepted view that predation is responsible for the maintenance of population size among vertebrates, believing that intraspecific competition demands more attention than it has received. Predation, in Errington's opinion, falls principally on the very young, the very old, and the diseased, i.e., on the insecure members of the population, who might otherwise have died in any event. Clearly, the task of constructing better life tables for natural populations, though an important prerequisite to the study of mortality, is not a substitute for such a study. Even so interesting a series of life tables as is available for *Balanus balanoides* proves to be unsatisfactory when it is realized that they all start at the same season, and the survivors are exposed to winter conditions at the same ages. What would happen to the survivorship curves if such animals were caused to be born out of season can only be found out by painstaking work. And until such questions, and many others, are answered, we will not be ready to establish a general theory of mortality.

"Sed omnes una manet nox
et calcanda semel via leti."

SUMMARY

Materials for the study of the age distribution of mortality are available from several natural populations of animals. Attempts are made, in most instances for the first time, to condense this information into life tables, showing for each age interval the number of deaths, the number of survivors, the mortality rate, and the expectation of further life of members of an initial cohort of 1000 individuals. These life table functions, especially when age is expressed in terms of units of the mean life span rather than in years, months, or days, should afford the best basis for comparing populations of the same and of different species in respect to their order of dying. Unfortunately, the ecological information is of unequal value in the various cases, and only limited and tentative comparisons can be made.

According to the methods used in collecting the information, the species studied fall into three groups: (a) those in which the *age at death* (d_x) is known, with fair accuracy, at least beyond certain ages (Dall mountain sheep, the sessile rotifer *Floscularia conifera*, and several species of birds); (*b*) those in which the *number of survivors* (l_x) out of a definite initial number has been directly observed at frequent intervals (barnacles, song sparrow, pheasant, snowshoe rabbit); (*c*) those in which the *age structure* (L_x) of the population is observed at a specified time, and the age at death is inferred from

the shrinkage between age classes (cormorant, many fish, fin whale). Information of type (*b*) is comparable to that obtainable from a laboratory experiment, provided only that the season of birth is sharply defined, and can be used without qualification for the construction of a life table. Information of types (*a*) and (*c*) can be so used only upon the assumption that the age structure of the population does not change with time.

Both in nature and in the laboratory, animals differ characteristically in their order of dying. When the mortality rate at all ages is constant, the survivorship (l_x) curve is diagonal on semi-logarithmic graph paper. Such a curve is found for many birds from adult stages onward; the mortality of adult birds is about 320 per thousand per hundred centiles of mean life span. If the constant age-specific mortality rate observed for the first few years of adult life is really maintained throughout life, the oldest bird in a cohort of 1000 lives 6.6 times as long as the average bird. Not all animals resemble birds in this respect, however, although many (e.g., fish) are assumed to do so. The Dall sheep, the rotifer, and possibly the barnacle are more like civilized man in that they seem to have evolved a mechanism for stretching the mean life span toward the maximum, so that the survivorship curve is convex. In these cases the maximum life span (among a sample of 1000) is only two or three times the mean. On the other hand there are undoubtedly species in which juvenile mortality is very heavy, but the few survivors to advanced ages die at reduced rates. This J-shaped or concave survivorship line, with the maximum longevity perhaps 15 or more times the mean, is presumed to characterize the oyster and other species, but it has not yet been formally recognized either in the laboratory or in nature. The closest approach to it, so far, is found when the survival of song sparrows is reckoned from the egg stage; but the mackerel will almost certainly provide an even better example.

Detailed comparisons between species cannot yet be made, partly because of the diverse statistical foundations of the life tables and partly because the data begin at different biological ages (birth, hatching, metamorphosis, sexual maturity, etc.) in the different cases. In all cases it is the youngest ages about which we know least, and ecologists should therefore concentrate their efforts on this segment of the life span of animals in nature.

The best examples of ecological life tables come from Hatton's work with the barnacle *Balanus balanoides*, which is a very favorable object for population research. By way of emphasizing the advantages of life table notation, Hatton's data are manipulated so as to show the relationship between longevity and population density. A theory of two-dimensional crowding by radially growing circular objects is first derived from geometric considerations, and it is then possible to relate the expectation of life (e_x) of a barnacle to a factor, called the *crowding coefficient*, which incorporates both the population density and the rate of growth. The number of barnacle populations available for study is limited, and Hatton's experiments were designed for a different purpose, but so far as the data go there is no evidence of an optimum density for survival of *B. balanoides*. Reasons are given for supposing that *Chthamalus stellatus* may prove to have such an optimum density.

ACKNOWLEDGMENTS

This article had its inception as part of a symposium, entitled "Life Tables and Their Application," held at Boston on December 27, 1943, under the joint auspices of the Ecological Society of America and the American Statistical Association. The present version has been completely reworked in the light of other contributions to the symposium. Remarks made at the meeting by Margaret Merrell, C. P. Winsor, and W. E. Ricker have been particularly helpful. Much has been learned also from later conversations with David Lack, G. E. Hutchinson, and Daniel Merriman. The author retains sole responsibility, however, for errors which may still remain.

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THE COMPARATIVE TOLERANCES OF SOME FOULING ORGANISMS TO COPPER AND MERCURY

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THE COMPARATIVE TOLERANCES OF SOME FOULING ORGANISMS TO COPPER AND MERCURY *

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The ability of marine organisms to attach to surfaces coated with ship-bottom paints depends on the toxicity of the surface and the sensitivity of the organisms to the toxic. Pyefinch (1946) presents a table showing the sensitivity of various organisms to toxics determined primarily from analysis of their settlement on toxic surfaces at Millport, Scotland. In the present studies carried out in the Biscayne Bay area, Florida, the tolerances of several common fouling organisms to copper and mercury have been compared by observations of the sequence of attachment to antifouling paints of moderate toxicity, to series of paints of graded toxicity, and to nontoxic surfaces adjacent to antifouling paint.

RESULTS

An indication of the relative tolerance of various organisms to toxic paints can be obtained by observing the frequency of their attachments to paints which are beginning to fail after long exposure. It may be expected that the most tolerant forms will be the first to attach. The organisms attaching earliest to each of 662 antifouling paints exposed at Miami Beach and Tahiti Beach, Florida, were recorded with the following result:

Barnacles	67%
Encrusting bryozoans	18
Hydroids	9
Erect bryozoans	5
Tunicates	1
Tubeworms	< 0.1
Sponges	< 0.1

The order of attachment depends not only upon the tolerance of the organisms to the toxics, but also upon their seasonal occurrences. For example, hydroids and those forms following them in the list attach first only when barnacles and encrusting bryozoans are absent from the fouling population. Encrusting bryozoans rank below barnacles because they are absent during a large part of the year, while barnacles are present at almost all times. One of the encrusting bryozoans, *Watersipora cucullata,* appears to be somewhat more tolerant to copper than the most tolerant barnacle species, *Balanus amphitrite,* since it frequently attached earlier when both organisms were present.

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The larva of a fouling organism which is unable to attach to a toxic paint surface may attach to a more resistant form which has already become established on the surface. Following this the adult may then spread over the paint surface. The relative tolerances of some fouling organisms to the toxic surfaces can frequently be assessed from these conditions of attachment.

The barnacles, *Balanus amphitrite* and *Balanus improvisus,* and the encrusting bryozoan, *Watersipora cucullata,* were found attached directly to paint surfaces. Attaching to and growing on these forms were *Schizoporella unicornis, Anomia* sp., *Bugula avicularia, Pennaria tiarella, Lepas anatifera* and tunicates. Examples of several of these organisms which were unable to attach to antifouling paints, but which attached to other forms on the paint, are shown in Figures 1–5.

A more precise evaluation of tolerance is given by comparing the frequency of attachment of different organisms on a surface of moderate toxicity with their frequency on a nontoxic control surface. A paint of moderate toxicity will allow attachment only of the forms having the highest tolerance to the paint toxics. Glass panels coated on one side with a paint in which cuprous oxide served as the toxic were exposed for periods of one month. The uncoated side served as a control. The use of the glass panel gave both surfaces the same color, thus eliminating any differential effect of color on attachment. Table I shows the numbers of barnacles of three species collected on these two surfaces. The total numbers of barnacles attaching to the toxic paint surface are less than one per cent of those growing on the nontoxic control. *Balanus amphitrite* comprises over 90 per cent of the population on the toxic surface, being the only barnacle species on most panels, though it is only 7.5 per cent of the population attaching to the control surface. In contrast *Balanus improvisus* makes up 90 per cent of the total attachment to the nontoxic surface but comprises only 9.4 per cent of the population on the paint. *Balanus eburneus* is completely inhibited from the toxic surface. It is thus evident that each of these three species of the same genus demonstrates a different degree of tolerance to the copper paint.

Table I

Total number of barnacles attached to 33 nontoxic and toxic surfaces (80 square inches in area) exposed for one month at intervals between October 1944 and May 1946

Barnacle species	Barnacles on nontoxic surface		Barnacles on toxic surface	
	Total	% of total	Total	% of total
Balanus improvisus	17,959	89.7	15	9.4
Balanus amphitrite	1,503	7.5	145	90.6
Balanus eburneus	564	2.8	0	0.0

In addition to the barnacle fouling the only other significant attachment to this paint surface was the encrusting bryozoan *Watersipora cucullata* and the green alga *Enteromorpha* sp. Both of these species attached only during the periods of their maximum abundance. On the nontoxic panels a total of twenty species of fouling

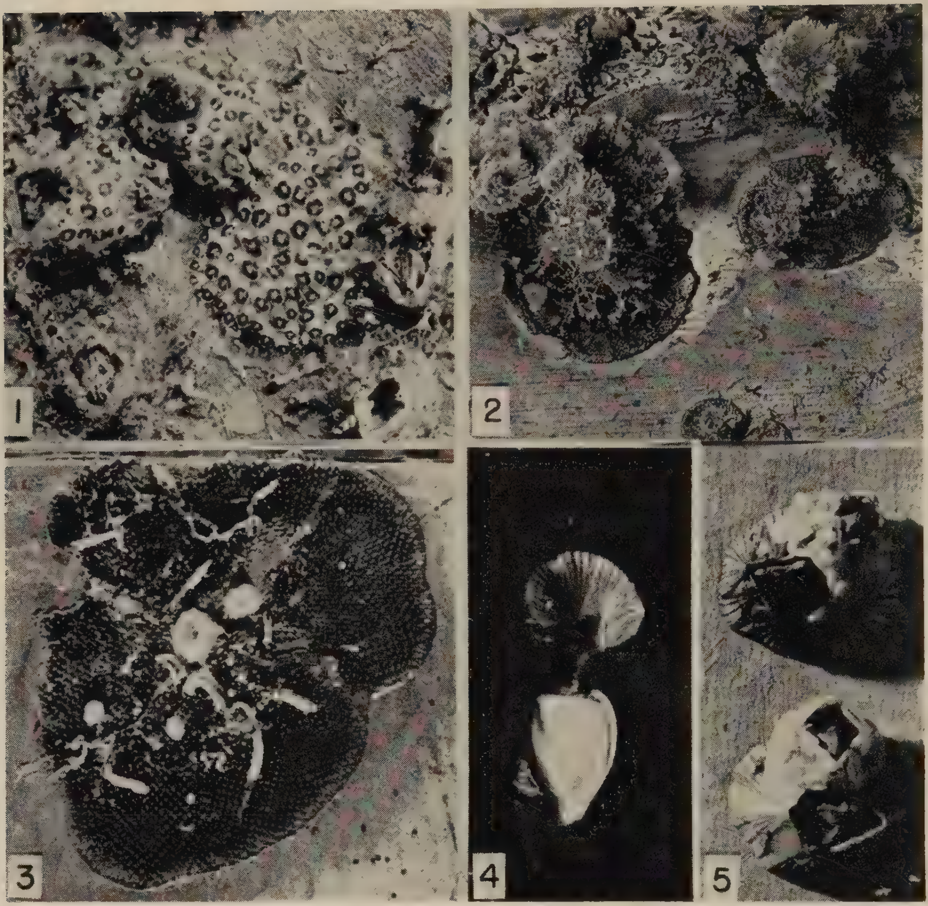

Plate I

Figure 1. A speckled tunicate limited in attachment to barnacles and *Anomia* sp. without spreading onto the paint surface.

Figure 2. *Bugula avicularia* attached to the encrusting bryozoan, *Watersipora cucullata*, which is growing directly on the paint.

Figure 3. Barnacles attached to *Watersipora cucullata* which developed directly on the paint surface. Tubes of *Dasychone conspersa* are also attached on *W. cucullata*.

Figure 4. Gooseneck barnacle, *Lepas anatifera,* attached to *Balanus amphitrite* which attached to an otherwise effective antifouling paint on a ship's bottom.

Figure 5. Two examples of *Balanus improvisus* which attached to the more resistant barnacle, *B. amphitrite*. Photographed after removal from the paint surface.

organisms attached during the period covered by these observations. These must be considered to be less tolerant than the four organisms which attached to the paint surface.

In order to establish the relative tolerances to copper of the more sensitive fouling forms a set of paints containing graded amounts of copper flake pigment was prepared. The copper leaching rates of these paints were measured as described by

Ketchum, Ferry, Redfield, and Burns (1945) and were found to vary in proportion to the pigment content and to decrease with the time of exposure. This series thus provided graded toxicities.

The relative tolerance of attaching organisms could be judged by the time of exposure elapsing before they attached to any one member of the series or by the number of members of the series which were fouled at any one time. The paints were applied to 8 × 10-inch weldwood panels which were immersed at Miami Beach and Tahiti Beach, Florida. The composition of the paints and the time of exposure before various fouling forms attached are given in Table II.

TABLE II

Number of months of exposure prior to appearance of fouling on painted panels immersed in the sea at Miami Beach, Florida (May 2, 1945–March 2, 1946), and at Tahiti Beach, Florida (May 2, 1945–September 2, 1945). The paints contained graded amounts of copper flake in a vehicle consisting of equal parts, by weight, of polyvinyl butyral and rosin.

Paint number Copper content, per cent dry weight	AF12 90	121 67	122 45	123 30	124 23	125 14
Miami Beach						
Balanus amphitrite	4	3	3	2	1	1
Watersipora cucullata	9	9	8	2	2	1
Balanus improvisus	a	a	a	a	2	1
Tahiti Beach						
Polysiphonia sp.	3	2	2	2	2	2
Balanus amphitrite	b	b	4	4	3	1
Hydroides parvus	b	b	b	4	4	3

a. None of this species had attached to these paints after 10 months of exposure.
b. None of these species had attached to these paints after 4 months of exposure.

At Miami Beach only three fouling organisms attached to the copper paints, two species of barnacles and the encrusting bryozoan *Watersipora cucullata*. Throughout the period of exposure there was no marked seasonal variation in the incidence of barnacles. However, seasonal fluctuation in the incidence of *Watersipora cucullata* accounts principally for the nonattachment of this organism between the second and ninth months of immersion of the paints. Its absence from the paints is, therefore, not indicative of its sensitivity to the paint toxic.

The exposure at Tahiti Beach, Florida, indicated that, on these copper paints, a red alga of the genus *Polysiphonia* is more tolerant, and that the tube worm, *Hydroides parvus*, is less tolerant than *Balanus amphitrite*.

Some species of fouling were too sensitive to attach even to the paints of lowest toxicity. To ascertain their relative tolerance of paint toxics their sequence of attachment was noted on nontoxic areas adjacent to paint surfaces. Observations by Miller (1946) on the diffusion of toxics from antifouling paints indicate that toxic gradients exist, decreasing from the paint edge. To provide nontoxic areas for attachment adjacent to the paint surfaces, strips 5, 10, and 20 mm. in width were left free of paint on the panels of the graded toxicity series.

At both exposure locations colonial tunicates attached to the widest bare strips on the paints of lowest toxicity, AF124 and AF125, by the second month of immersion.

By the third and fourth months of exposure hydroids had attached to the initial fouling on these nontoxic areas. These observations indicate that tunicates are more tolerant than hydroids to copper but less tolerant than those forms able to attach directly to the paint surface.

From the preceding observations several fouling forms can be arranged in order of decreasing tolerance to copper as follows: *Polysiphonia* sp., *Watersipora cucullata, Balanus amphitrite, Balanus improvisus, Balanus eburneus, Hydroides parvus,* tunicates and hydroids.

In the examination of antifouling paints employing mercury pigments or mixtures of mercury and copper pigments as the toxic ingredients, it was noted that certain of the fouling organisms appeared to be more sensitive to mercury than to copper while for others the reverse was true.

To establish the comparative tolerance of different species to mercury a series of paints containing mercurous chloride in graded concentration was made. The vehicle was the same as that used for the copper series. The mercury content of these paints was equal in weight to the corresponding member of the copper series. These paints were immersed simultaneously and at the same locations as the copper paints. The extent of exposure before fouling attached to the paint surfaces of the AF12 mercury series is shown in Table III.

TABLE III

Number of months of exposure prior to appearance of fouling on painted panels immersed in the sea at Miami Beach, Florida (May 2, 1945–March 2, 1946), and at Tahiti Beach, Florida (May 2, 1945–September 2, 1945). The paints contained graded amounts of mercury, added as mercurous chloride, in the vehicle described in Table II.

Paint number Mercury content, per cent dry weight	AF12 90	121 67	122 45	123 30	124 23	125 14
Miami Beach						
Balanus amphitrite	9	9	2	2	2	1
Balanus improvisus	a	a	a	4	9	2
Bugula neritina	a	a	a	2	6	1
Watersipora cucullata	a	a	a	6*	a	4*
Tahiti Beach						
Polysiphonia sp.	b	b	b	3	3	1
Balanus amphitrite	b	b	b	b	2	2

a. None of these species had attached to these paints after 10 months of exposure.
b. None of these species had attached to these paints after 4 months of exposure.
* Single specimen not present on following month.

At Miami Beach four organisms attached to this series of paints. The most resistant of these was *Balanus amphitrite,* followed in order by *B. improvisus* and *Bugula neritina. Watersipora cucullata,* which was found to be quite tolerant of copper, attached to only two of these paints, and in neither case was the attachment secure. In contrast, *Bulgula neritina* was able to attach directly to the mercury paints but was never found on any of the comparable copper paint surfaces. At Tahiti Beach *Polysiphonia* sp. was found to be more tolerant than *Balanus amphitrite* to the mercury paints.

Photographs of two of the copper and two of the mercury paints of these series, after nine months of exposure at Miami Beach, are shown in Figure 6. The ability of *Watersipora cucullata* to attach to the copper paints and its absence from the comparable mercury paints are shown. Both of the copper paints and one of the mercury paints are fouled with *Balanus amphitrite*.

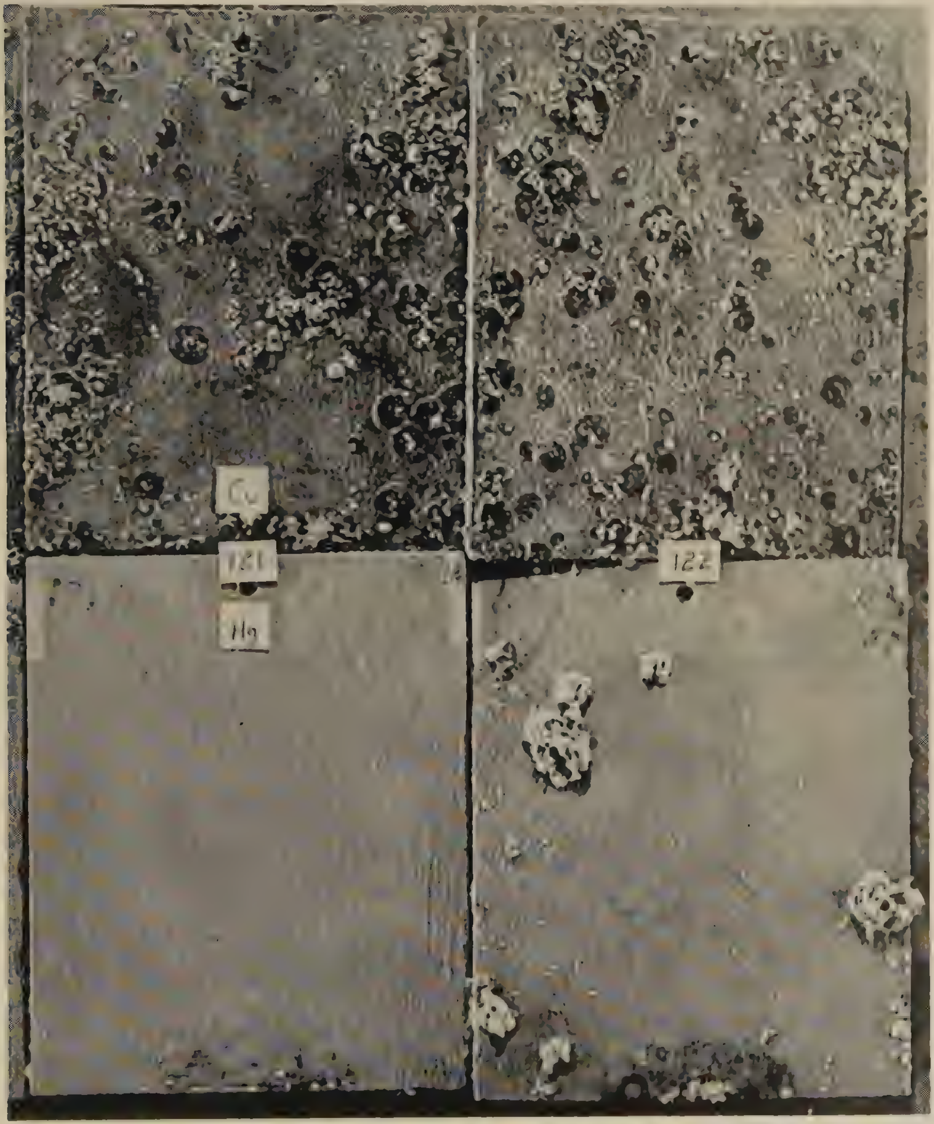

Plate II

Figure 6. Comparison of the attachment of *Watersipora cucullata* to paints pigmented with copper and mercury after nine months of exposure. *W. cucullata* appears on the copper series (top panels) as the dark disc-like organisms.

Nontoxic strips on panels otherwise coated with the mercury paints permitted attachment of the more sensitive fouling forms. The more resistant forms mentioned above always attached first to these nontoxic areas. In addition, *Watersipora cucullata, Anomia* sp., hydroids and tunicates invaded the unpainted areas at Miami Beach. At Tahiti Beach *Enteromorpha* sp. and *Hydroides parvus* attached in the order given.

These exposures indicate the following order of decreasing tolerance of some fouling organisms to mercury as a paint toxic: *Polysiphonia* sp., *Balanus amphitrite, Bugula neritina, Balanus improvisus, Watersipora cucullata, Anomia* sp., *Enteromorpha* sp., *Hydroides parvus,* hydroids and tunicates.

From the results of the various methods described above the comparative tolerance of several fouling organisms to copper and mercury has been evaluated. The results are given in Table IV. The organisms listed as attaching to adjacent nontoxic surfaces include those which may on occasion be found on paints of low toxicity but which generally do not attach directly to the paint surface. The exact position in the order of decreasing tolerance, for all but the first three organisms in each column, requires further verification.

TABLE IV

The comparative tolerance of some fouling organisms of the Biscayne Bay area, Florida, to copper and mercury employed as pigments in antifouling paints. The lists are arranged in approximate order of decreasing tolerance.

	Copper	Mercury
Organisms found attached to toxic paint surfaces	*Polysiphonia* sp. *Watersipora cucullata* *Balanus amphitrite* *Enteromorpha* sp. *Balanus improvisus* *Balanus eburneus* *Hydroides parvus*	*Polysiphonia* sp. *Balanus amphitrite* *Bugula neritina* *Balanus improvisus* *Watersipora cucullata*
Organisms found mainly attached to nontoxic areas adjacent to paint surfaces	*Anomia* sp. *Bugula neritina* *Bugula avicularia* *Lepas anatifera* tunicates hydroids	*Anomia* sp. *Enteromorpha* sp. *Hydroides parvus* hydroids tunicates

DISCUSSION

Relatively few of the sessile species in the Miami area which attach to neutral surfaces are able to attach to antifouling paints. Even paints of such low toxicity that they become completely covered permit the attachment of only four or five forms. Many less resistant fouling organisms are excluded from the paint surface. Effective antifouling paints must be designed to prevent the attachment of the few most tolerant forms.

The species most tolerant of copper are different from those most resistant to mercury. The conflicting opinions which have existed concerning the relative efficiencies of copper and mercury compounds as paint toxics may depend largely on the species of fouling organisms present at the particular testing location.

The present results and those given by Pyefinch (1946) agree in showing that *Enteromorpha* and *Polysiphonia* are among the more resistant forms, and *Anomia* and tunicates have low tolerance to paint toxics. Tubularian hydroids were noted only as secondary fouling at Miami, though Pyefinch rates them more resistant than *Balanus* and equal to *Enteromorpha*. A direct comparison of the results with *Balanus* is not feasible since the three species found in Miami showed marked differences in toxic sensitivity. None of these species are found at Millport where Pyefinch's studies were made. Pyefinch lists a greater variety of algae, including diatoms, which were not included in the investigations at Miami.

Summary

The comparative toxic tolerance of several fouling organisms was based on the sequence of their attachment to copper and mercury antifouling paints. A red alga, *Polysiphonia* sp., and the barnacle, *Balanus amphitrite,* were the most tolerant and attached to copper and mercury paints before other organisms. The encrusting bryozoan, *Watersipora cucullata,* was found to be slightly more tolerant to copper but considerably less tolerant to mercury than the above two forms. Less tolerant forms were *Balanus improvisus, Hydroides parvus, Bugula neritina, Anomia* sp., *Enteromorpha* sp., tunicates and hydroids. Other species, though attaching to nontoxic surfaces, were never found on the toxic paints.

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Contribution No. 386

Transactions, American Geophysical Union Volume 28, Number 5 October 1947

INVESTIGATION OF UNDERWATER PRESSURE RECORDS AND SIMULTANEOUS SEA SURFACE PATTERNS

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(Contribution No. 386, Woods Hole Oceanographic Institution)

Abstract--An investigation to determine the extent to which underwater pressure recordings may be used to characterize sea-surface conditions has been in process during the past six months. On the basis of information derived from consistent photographic recordings of sea-surface patterns and simultaneous underwater pressure records at Woods Hole and Bermuda, it appears possible to derive the average interference pattern of the sea surface from the underwater recordings.

In the latter part of 1946, a quantitative investigation of relationships between sea-surface wave patterns and underwater pressure records was started at the Woods Hole Oceanographic Institution. At that time, an underwater pressure recorder, developed under Navy Contract NObs-2083, was in operation off Cuttyhunk Island; and in November a second pressure recorder was installed off Bermuda. (These underwater pressure recorders were designed and built by A. A. Klebba at the Woods Hole Oceanographic Institution.) To obtain sea-surface data for comparison it was only necessary to observe sea-surface wave heights and periods immediately over the instruments.

The underwater pressure recorder off Cuttyhunk was located at a depth of 75 feet and that off Bermuda at 120 feet. In both cases pressure impulses near the bottom were electrically transmitted to clockwork recorders installed on shore several miles away. Comparative data on the state of the sea immediately overhead were obtained by photographing changes in sea surface against a fixed, floating, graduated pole, using a 16 mm motion picture camera. The graduated pole was anchored near the underwater instrument and synchronization of surface and bottom observations was obtained by exploding a small charge of TNT near the surface while the camera was in operation. This produced a geyser at the surface to be recorded on the photographic film, and a tick on the underwater recorder record. A total of three experiments provide the data for this investigation. Field data for the experiments are outlined in Table 1.

Table 1--Field experimental data, and average height and period of sea surface during observational time

No. Location Date	Photo run	Starting time	Frames exposed	Total time	Average height	Average period
		h m s		h m	ft	sec
1	1	10 58 21	761			
Cuttyhunk	2	11 10 32	759			
June 14, 1946	5	11 48 52	759			
	6	12 01 26	570	01 04	1.19	4.34
2	1	10 33 30	759			
Cuttyhunk	2	10 48 51	759			
June 27, 1946	3	10 52 07	754			
	5	11 11 01	758			
	6	11 21 39	760	00 49	1.42	3.16
5	1	14 53	700			
Bermuda	2	14 57	740			
October 25, 1946	5	15 12	740	00 20	1.5	3.0

The purpose of the investigation was to test (for the two localities concerned) the adequacy of the theory relating surface and bottom pressure fluctuations in the sea. According to hydrodynamic theory, for irrotational wave motion, pressure fluctuations arising from wave height variations of the sea surface should diminish as they are propagated vertically downward. The damping of pressure fluctuations with depth appears to be a function of wave period and depth. At or near the bottom the amplitude of the resulting pressure fluctuation is related to that at the surface as follows:

$$\Delta P_h/\Delta P_s = 1/\cosh kh \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (1)$$

Hence, pressure fluctuations, recorded by means of instruments either suspended in the sea, or resting on the bottom, are not identical with those of the overlying sea surface. The damping phenomenon is selective to the extent that longer period waves, usually obscured at the sea surface, become recognizable in underwater pressure records.

The ratios of bottom to surface pressure fluctuations for the three experiments were computed from direct comparison of individual wave heights of surface and bottom profiles. In Figure 1 they are compared with theoretical values of Equation (1), where it is indicated that the relationship expressed by (1) is not adequate in that pressure fluctuations at the surface computed by means of the relation indicated above are too low.

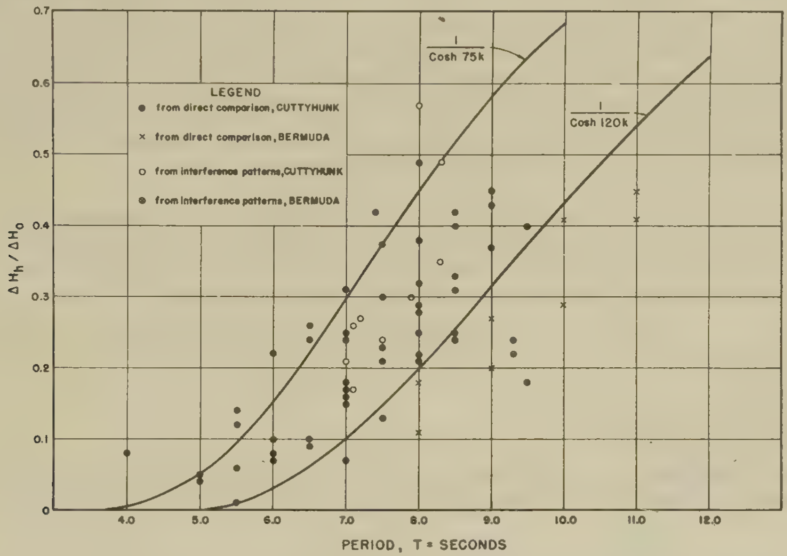

Fig. 1--Ratios of bottom to surface pressure fluctuations ($\Delta H_h/\Delta H_0$) as indicated; theoretical curves for Cuttyhunk (75 foot depth) and Bermuda (120 foot depth), without empirical correction

Table 2--Summary of bottom-surface fluctuation ratios ($\Delta H_h/\Delta H_s$) from interference patterns (IP) and from direct comparison of observations (0), compared with theoretical bottom-surface ratios from Equation (1) ($\Delta P_h/\Delta P_s = 1/\cosh kh$)

Experiment	Range $\Delta P_h/\Delta P_s - \Delta H_h/\Delta H_s$	Average $\Delta P_h/\Delta P_s - \Delta H_h/\Delta H_s$	Average $(\Delta P_h/\Delta P_s)/(\Delta H_h/\Delta H_s)$
1 and 2 (IP)	- 0.13 to + 0.15	0.11	1.31
1 and 2 (0)	- 0.07 to + 0.28	0.12	1.37
5 (IP and 0)	- 0.02 to + 0.20	0.10	1.37
Average	.	0.11	1.35

Average results for all experiments are given in Table 2, where statistics showing average differences between theoretical, $\Delta P_h/\Delta P_s$, and observed values, $\Delta H_h/\Delta H_s$, and the average ratios of theoretical to computed values, $(\Delta P_h/\Delta P_s)/(\Delta H_h/\Delta H_s)$, are reasonably constant for all experiments. The fact that this should occur for the two locations, 750 miles apart, with different hydrographic characteristics, at bottom depths of 75 and 120 feet, and with observation times four months apart, leads to the conclusion that the average ratios possess empirical significance.

The average ratio of theoretical $\Delta P_h/\Delta P_s$ to computed $\Delta H_h/\Delta H_s$ values was 1.35. Hence, the theoretical relationship, $\Delta P_h/\Delta P_s$, is according to our observations, 1.35 times the observed relationship, $\Delta H_h/\Delta H_s$, or

$$\Delta P_h/\Delta P_s = 1.35\ \Delta H_h/\Delta H_s \qquad (2)$$

and

$$\Delta H_s = 1.35\ \Delta H_h[1/(\Delta P_h/P_s)] \qquad (3)$$

Substituting (1) in (3), we have

$$\Delta H_s = 1.35\ \Delta H_h \cosh kh \qquad (4)$$

as the general equation for estimating sea-surface fluctuations from underwater pressure records. The depth of the pressure recording instrument near the bottom is h. Use of this equation is, for the present, restricted to measurements in the vicinity of Woods Hole and Bermuda.

Based on the present investigation, it is recommended that average sea-surface conditions be computed from underwater pressure-recorder records as follows. Two minute intervals are selected from the underwater recorder tape and average period, average crest height and macimum crest height and its period are computed. To compute average and maximum heights of the overlying sea surface, these values are multiplied by 1.35 times cosh kh. This recommendation, based on equipment in use at this Institution, where the underwater recorder is in operation 20 minutes out of every four hours, has been found satisfactory.

It should be noted that the average period of the sea surface will be somewhat less than the average period of the record depending on depth of the recorder. Thus, for Cuttyhunk the average period of pressure fluctuations near the bottom was about twice that of the surface, whereas at Bermuda, the bottom average was about three times that at the surface.

A complete report, including field and analytical mathods of this investigation, will be published in the near future.

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VISCOSITY AND THERMAL CONDUCTIVITY OF AIR AND DIFFUSIVITY OF WATER VAPOR IN AIR

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(Manuscript received 23 May 1947)

ABSTRACT

Carefully chosen numerical values for the viscosity and thermal conductivity of air and diffusivity of water vapor in air are tabulated for temperatures from −20C to +40C and for a pressure of 1000 mb. A summary of physical constants relating to air is included.

Different reference books disagree rather widely with regard to numerical values for the viscosity, conductivity, and diffusivity of air. Since these quantities are of basic importance in a wide variety of problems concerning the meteorology of the surface layer, a summary has been prepared of the most reliable values available to date. Viscosity, conductivity, and diffusivity are presented in a uniform manner. The 'kinematic' quantities, which depend on pressure, are reduced to a standard pressure of 1000 mb for convenience in meteorological problems.

Since nearly all measurements have been made at room temperature and higher, the values presented for the lower temperatures result from extrapolation. The diffusivity of water vapor in air is relatively uncertain at all temperatures. Further measurements are desirable.

1. Dynamic viscosity

The dynamic viscosity μ, having dimensions $L^{-1}MT^{-1}$, may be defined as the ratio of shearing stress to shear, so

$$\tau = \mu\, \partial u/\partial z,$$

where τ is stress and $\partial u/\partial z$ is shear. The basic cgs unit is 1 poise = 1 g cm^{-1}s^{-1}. The dynamic viscosity of a gas is independent of pressure except at very low pressures. Its dependence on temperature is well represented by Sutherland's equation (Licht and Stechert, 1944), which may be written

$$\frac{\mu}{\mu_0} = \frac{T_0 + C}{T + C}\left(\frac{T}{T_0}\right)^{\frac{3}{2}},$$

where T is absolute temperature and μ_0 is the viscosity at absolute temperature T_0. Sutherland's constant C for air has the value 120C according to Bircumshaw and Stott (1929).

A number of highly accurate measurements of the viscosity of air at room temperature have been carried out recently because they were required for the determination of the electronic charge by Millikan's oil-drop method. Birge (1945) concludes from these that the viscosity of air at 23C is

$$(1.8325 \pm 0.0010) \times 10^{-4}\ \mathrm{g\ cm^{-1}s^{-1}}.$$

The values of dynamic viscosity in table 1 have been computed from Sutherland's equation by use of the two constants presented above and 273.16C for the absolute temperature of the ice point (Birge, 1941).

For comparison with Bircumshaw and Stott's value of Sutherland's constant, the following three measurements may be cited: 119.4C in the temperature range 15–302C by Breitenbach (1901), 123.6C in the range 17–477C by Braune, Basch, and Wentzel (1928), and 111C in the range 20–830C by Trautz and Zink (1930). Brémond's (1933) measurements of the viscosity of air in the temperature range 18–1134C agree closely with Breitenbach's value of 119.4C for Sutherland's constant. Two recent measurements of $d\mu/dT$ are 4.93×10^{-7} g cm^{-1}s^{-1}C^{-1} by Ridgen (1938) in the short range 15–19C and 4.95×10^{-7} g cm^{-1}s^{-1}C^{-1} by Banerjea and Pattanaik (1938). These may be compared with values computed from Sutherland's equation:

Sutherland's constant, C	Temperature	$d\mu/dT$
120C	0C	5.06×10^{-7} g cm^{-1}s^{-1}C^{-1}
120	20	4.90
110	20	4.79

From the six series of measurements it appears probable that the error in the value 120C for Sutherland's constant does not exceed 5C. This corresponds to an error in the viscosity in table 1 amounting, for the lowest temperature, to 2½ in the last place.

The determinations of Sutherland's constant are all based on measurements at and above room temperature, so the values in table 1 for viscosity at −20C to +10C represent extrapolations. The viscosity of air

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[1] Contribution No. 388.

TABLE 1. Dynamic viscosity and thermal conductivity of air.

Temperature C	Dynamic viscosity μ g cm^{-1}s^{-1} = poise	Thermal conductivity k cal cm^{-1}s^{-1}C^{-1}	 erg cm^{-1}s^{-1}C^{-1}
−20	1.615×10^{-4}	5.45×10^{-5}	2.28×10^{3}
−10	1.667	5.63	2.36
0	1.718	5.80	2.43
10	1.768	5.97	2.50
20	1.818	6.14	2.57
30	1.866	6.30	2.64
40	1.914	6.46	2.70

at −21C was measured by Breitenbach (1901), but he neglected this measurement in determining Sutherland's constant; the measured value is 0.016×10^{-4} g cm^{-1}s^{-1} higher than his value computed from Sutherland's formula. The values of viscosity in Keenan and Kaye's (1945) table 3 at −20C to +10C are about one per cent greater than those in the present table 1. Keenan and Kaye do not explain clearly the source of their values at low temperatures (Breitenbach?); there appears to be no reason to prefer their tabulation to the present one.

2. Kinematic viscosity

The ratio of dynamic viscosity to density ρ is the kinematic viscosity, $\nu = \mu/\rho$, having dimensions L^{2}T^{-1}. It is the factor occurring in the relation giving the acceleration du/dt due to fluid friction. In the simplest case this relation is of the type

$$\frac{du}{dt} = \nu \frac{\partial^2 u}{\partial z^2}.$$

The values of kinematic viscosity in table 2 have been computed from dynamic viscosity and density. By use of the equation of state for a perfect gas, the density has been computed from 1.2930×10^{-3} g cm^{-3} as the density of air at 0C and 1 atmosphere (*Smithsonian meteorological tables*, 5th ed., p. xlvi; see also Guye, 1917) and from 1013.25 mb as the equivalent of 1 atmosphere (Birge, 1941).[2] The density values also are listed in table 2.

TABLE 2. Density, kinematic viscosity, and thermometric conductivity of air and diffusivity of water vapor in air, at 1000 mb.

Temperature C	Density ρ g cm^{-3}	Kinematic viscosity ν cm^{2}s^{-1}	Thermometric conductivity ν_c cm^{2}s^{-1}	Diffusivity D cm^{2}s^{-1}
−20	1.3769×10^{-3}	0.1173	0.165	0.197
−10	1.3246	.1259	.177	.211
0	1.2761	.1346	.189	.226
10	1.2310	.1437	.202	.241
20	1.1890	.1529	.215	.257
30	1.1498	.1623	.228	.273
40	1.1131	.1720	.242	.289

3. Thermal conductivity

The thermal conductivity k is the absolute value of the ratio of H, the rate of heat conduction per unit area, to the temperature gradient, so

$$H = -k\, \partial T/\partial z.$$

It has the same dimensions as the product of dynamic viscosity and specific heat. Like dynamic viscosity, it depends on temperature but not on pressure.

The value of the thermal conductivity of air at 0C given in the compilation by Chapman and Cowling (1939, table 22) is 5.80×10^{-5} cal cm^{-1}s^{-1}C^{-1}. Measurements have not been made below 0C. According to Chapman and Cowling (1939, p. 242), its variation "with temperature is in general approximately the same as the variation of the coefficient of viscosity." The values in table 1 are therefore based on Chapman and Cowling's value at 0C and on a constant ratio μ/k. The values in mechanical units result from the conversion 1 cal$_{15\text{C}}$ = 4.1855×10^7 erg (Birge, 1941).

Keenan and Kaye (1945, table 3) find that the Prandtl number, $\sigma = c_p\mu/k$, where c_p is the isobaric specific heat, decreases from 0.71 at 0C to 0.70 at 40C and to 0.66 at 300C, the highest temperature at which the thermal conductivity had been measured. From 0C to 40C the Prandtl number therefore decreases by 1½ per cent, while their values of thermal conductivity increase by 13 per cent (and their values of isobaric specific heat increase by only 0.2 per cent); hence nine tenths of the change in the thermal conductivity is accounted for by the change in viscosity. Although Keenan and Kaye extrapolate thermal conductivity below 0C by means of a variable Prandtl number, the use of a constant ratio μ/k appears to yield more reliable values in the comparatively short range from −20C to +40C.

Chapman and Cowling's value adopted here for the thermal conductivity of air at 0C is 7 per cent greater than the old value in the *International critical tables* (Laby and Nelson, 1929). The values in table 1 are, however, supported by the following measurements in addition to those cited by Chapman and Cowling: 5.810×10^{-5} cal cm^{-1}s^{-1}C^{-1} at 0C (extrapolated from 4C) and 5.965×10^{-5} cal cm^{-1}s^{-1}C^{-1} at 10C, both by Milverton (1934), and $(6.06 \pm 0.04) \times 10^{-5}$

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[2] The universal gas constant is

$$R = 8.3144 \times 10^7 \text{ erg C}^{-1}\text{mole}^{-1}$$

according to Birge (1941), so the mean molecular weight of dry air from the equation of state,

$$p = (R/m)\rho T,$$

where p is pressure, is consequently $m_d = 28.982$. Since the equation of state is not exactly satisfied even by dry air, this value is not exactly the same as the mean molecular weight computed from the chemical composition of dry air; rather, the value $m_d = 28.982$ is so chosen that the equation of state for dry air is identically satisfied at 0C and 1 atmosphere. The molecular weight of water from Birge's atomic weight of hydrogen is $m_w = 18.01600$, so the ratio of the molecular weights is $m_w/m_d = 0.6216$.

cal $\mathrm{cm^{-1}s^{-1}C^{-1}}$ at 20C by Hercus and Sutherland (1934; see also Laby, 1934). For comparison, values interpolated and converted from the table of Keenan and Kaye are, for the temperatures in table 1, 2.28, 2.36, 2.44, 2.52, 2.60, 2.68, and 2.76×10^3 erg $\mathrm{cm^{-1}s^{-1}C^{-1}}$, respectively. The probable error estimated by neglecting the older determinations yields $(5.80 \pm 0.02)10^{-5}$ cal $\mathrm{cm^{-1}s^{-1}C^{-1}}$ as the thermal conductivity of air at 0C.

4. Thermometric conductivity

The rate of heating due to a given temperature distribution depends on the thermometric conductivity, $\nu_c = k/(c_p\rho)$:

$$\frac{dT}{dt} = \nu_c \frac{\partial^2 T}{\partial z^2}.$$

Its dimensions are the same as for kinematic viscosity, namely, L^2T^{-1}. The value for 0C, 0.1895 $\mathrm{cm^2s^{-1}}$, has been computed from the thermal conductivity by use of 1.004×10^7 erg $\mathrm{g^{-1}C^{-1}}$ for the isobaric specific heat of air (Leduc, 1929).[3] The ratio μ/k has been assumed constant for air, and the same may be assumed of specific heat, so the ratio ν/ν_c also is constant. The values of thermometric conductivity at temperatures other than 0C have therefore been computed from the corresponding values of kinematic viscosity.

5. Diffusivity

A substance having the concentration (mass per total mass) q in a mixture of density ρ is diffused at the rate, in mass per unit area and time,

$$E = -\rho D\, \partial q/\partial z,$$

where D is the diffusivity, dimensions L^2T^{-1}. The corresponding rate of change of concentration is

$$\frac{dq}{dt} = D\frac{\partial^2 q}{\partial z^2}.$$

For gases the dependence of diffusivity on pressure and temperature is represented (Boynton and Brattain, 1929) by

$$\frac{D}{D_0} = \left(\frac{T}{T_0}\right)^n \frac{p_0}{p},$$

where D_0 is the diffusivity at absolute temperature T_0 and at pressure p_0. For any given temperature the diffusivity is therefore inversely proportional to pressure, just as are kinematic viscosity and thermometric conductivity. For a change at constant pressure,

$$\frac{d}{dT}\ln\frac{D}{D_0} = \frac{n}{T}.$$

The corresponding variation of kinematic viscosity, according to Sutherland's equation and the equation of state for a perfect gas, is

$$\frac{d}{dT}\ln\frac{\nu}{\nu_0} = \frac{5}{2}\frac{1}{T} - \frac{1}{T+C};$$

at 0C this quantity has the value 0.00661 $\mathrm{C^{-1}}$ (based on $C = 120\mathrm{C}$). The most reliable determination of the diffusivity of water vapor in air is presumably that of Schirmer (1938), who gives $n = 1.81$. At 0C, therefore, $n/T = 0.00663\ \mathrm{C^{-1}}$, practically identical with the corresponding value for kinematic viscosity. It therefore follows that the variation with temperature in the neighborhood of 0C, as well as with pressure, is the same for diffusivity as for kinematic viscosity.

The values of diffusivity in table 2 are based on Schirmer's value of 0.083 $\mathrm{m^2hr^{-1}}$ for 0C and for a pressure of 1 kg(force) $\mathrm{cm^{-2}}$, which is 980.665 mb; his value corresponds to 0.226 $\mathrm{cm^2s^{-1}}$ at 1000 mb. The values of diffusivity at other temperatures have been computed from the kinematic viscosity, to which they are proportional.

For comparison, the diffusivity of water vapor in air at 0C according to the *International critical tables* (Boynton and Brattain, 1929) is 0.220 $\mathrm{cm^2s^{-1}}$ at 1 atmosphere and corresponds to 0.223 $\mathrm{cm^2s^{-1}}$ at 1000 mb; n is stated to be 1.75. Trautz and Müller (1935a; 1935b) deduce a value (0.219 ± 0.001 $\mathrm{cm^2s^{-1}}$ at 1 atmosphere) corresponding to 0.222 $\mathrm{cm^2s^{-1}}$ at 0C and 1000 mb, and give $n = 1.853$. These two values agree closely with Schirmer's. Summerhays (1930) measured 0.282 $\mathrm{cm^2s^{-1}}$ at 16.1C, which reduces, if the measurement was at 1 atmosphere, to 0.293 $\mathrm{cm^2s^{-1}}$ at 20C and 1000 mb; this measurement results in a value 14 per cent higher than that in table 2. These three values, but not Schirmer's, are listed by Dorsey (1940, pp. 72–73). A probable error estimated by neglecting Summerhays's measurement yields

$$(0.226 \pm 0.003)\ \mathrm{cm^2s^{-1}}$$

as the diffusivity of water vapor in air at 0C.

6. Nondimensional ratios

Ratios of quantities in table 2 are dimensionless and are nearly independent of temperature and pressure. The Prandtl number, which is the ratio of kinematic viscosity to thermometric conductivity, has the value at 0C

$$\sigma = \nu/\nu_c = c_p\mu/k = 0.711 \pm 0.003.$$

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[3] This value agrees with

$$0.2399\ \mathrm{Btu\ lb^{-1}F^{-1}} = 1.0045 \times 10^7\ \mathrm{erg\ g^{-1}C^{-1}}$$

resulting from a new summarization by Keenan and Kaye (1945, table 3). Their table shows the variation of specific heat with temperature over a wide range.

It may be noted that Leduc's value of specific heat, together with the values of the universal gas constant and the mean molecular weight given above, determines the value of the Poisson constant for dry air to be $R/(mc_p) = 0.286$.

The ratio of kinematic viscosity to diffusivity at 0C is

$$\nu/D = 0.596 \pm 0.008,$$

and the ratio of thermometric conductivity to diffusivity at 0C is

$$\nu_c/D = 0.84 \pm 0.01.$$

7. Summary of constants

The various constants used in computing the values presented above have been chosen with care and are more precise than the ones to be found in common meteorological reference works. The summary below may therefore be useful.

Absolute temperature of the ice point (Birge, 1941): 273.16C ± 0.01C.

1 atmosphere = 1013.246 mb ± 0.004 mb (Birge, 1941) = 1013.25 mb.

Density, at 0C and 1 atmosphere, of dry air containing an average amount of carbon dioxide: $(1.2930 \pm 0.0001)10^{-3}$ g cm^{-3}.

Universal gas constant (Birge, 1941): $R = (8.3144 \pm 0.0004)10^7$ erg C^{-1}mole^{-1}.

Mean molecular weight of dry air (derived from preceding constants): $m_d = 28.982 \pm 0.003$.

Molecular weight of water (Birge, 1941): $m_w = 18.01600 \pm 0.00004$.

$m_w/m_d = 0.6216 \pm 0.0001$.

Isobaric specific heat of dry air at 0C: $c_p = (1.004 \pm 0.001)10^7$ erg g^{-1}C^{-1}.

Poisson constant for dry air: $R/(mc_p) = 0.286$.

1 cal$_{15C}$ (Birge, 1941) = $(4.1855 \pm 0.0004)10^7$ erg.

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Contribution No. 396

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NOTES ON THE DIET OF THE GOOSEFISH, *LOPHIUS AMERICANUS*.[1]—There is perhaps no fish along our North Atlantic coast that has a more voracious appetite or consumes a greater variety of food than the goosefish, or angler. It ranges along the coast of eastern North America from the Newfoundland Banks to North Carolina and, in deep water, still further southward. A specimen caught by the research vessel *Atlantis* on the south coast of Cuba has yet to be compared with *americanus*.

The diet of the goosefish includes many species of fishes such as eels, herrings, mackerel, cod, haddock, hakes, sculpins and flatfishes. Any fish it can catch doubtless finds its way into the capacious stomach. It also is known to have captured birds such as cormorants, loons and gulls as well as a long list of invertebrates, and Bigelow and Welsh (1924, U. S. Bureau of Fisheries, Bulletin, Pt. 1) state that "in short, nothing edible that strays within reach comes amiss."

Varied as is its diet, marine turtles have not as yet been included in the list of foods, hence it is of interest to report that, on June 10, 1944, Mr. Marcus Conlan found a goosefish on the shore of Nonamesset Island, off Woods Hole, Massachusetts, which had in its stomach a specimen of Kemp's turtle (*Lepidochelys kempi* Garman) that had a carapace 9¾ inches in length. It is evident that the turtle was much too large and indigestible for the goosefish and was the direct cause of its death.

Another instance of this sort came to my attention in 1925 during a cod tagging cruise of the U. S. Bureau of Fisheries Steamer *Halcyon*. On Nantucket Shoals we gaffed a slowly swimming *Lophius* which proved to be 3 feet long and had in its stomach a haddock 31 inches long, so large that it evidently prevented the goosefish from leaving the surface because of the gases produced during the slow process of digestion.

It is also of interest to note that this 31-inch haddock was of an extraordinary size, for of about 15,000 caught with hand lines during the cod investigation, from 1923 to 1932, between Cape Sable, Nova Scotia, and Nantucket Shoals, only about 100 exceeded 30½ inches in total length.—WILLIAM C. SCHROEDER, *Woods Hole Oceanographic Institution, Woods Hole, Massachusetts.*

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[1] Contribution No. 396 from Woods Hole Oceanographic Institution.

Contribution No. 397

MAXIMUM AND MINIMUM MONTHLY MEAN SEA SURFACE TEMPERATURES CHARTED FROM THE "WORLD ATLAS OF SEA SURFACE TEMPERATURES"[1]

BY

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Woods Hole Oceanographic Institution

INTRODUCTION

Maximum and minimum water temperatures are of interest in oceanography in many connections. Among their more important uses, they afford the most valuable simple index of temperature conditions for analyses of the distributions of marine organisms.

The "World Atlas of Sea Surface Temperatures," issued by the Hydrographic Office (1944) of the United States Navy Department, incorporates a large share of the previously published temperature data, together with records in the Hydrographic Office files totalling in the millions. Since the Atlas is therefore the most comprehensive treatment of surface temperatures available, and is likely to be a standard reference for some time, preparation of maximum and minimum charts conforming to its data seemed desirable. Such charts are given here in Plates I and II. The method of preparing them is described below, followed by some comments on the degree of reliability which should be accorded them and the Atlas.

METHOD OF PREPARATION

The Atlas plots the isotherms of monthly mean temperatures of even 5° F. intervals, giving monthly charts for the Atlantic, eastern Pacific, western Pacific and Indian Ocean sectors of the globe. Isotherms for intermediate 2½° F. values are also given for some months in some regions, but these have not been used here.

From the monthly Atlas sheets for an ocean, a separate map was traced for each 5° temperature value, superimposing the courses of all its isotherms during the twelve months. Figure 69 illustrates the procedure with the isotherms of 75° F. in the South Atlantic. The whole area occupied at any time during the year by a particular monthly mean temperature was thereby determined. The distribu-

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[1] Contribution No. 397 from the Woods Hole Oceanographic Institution.

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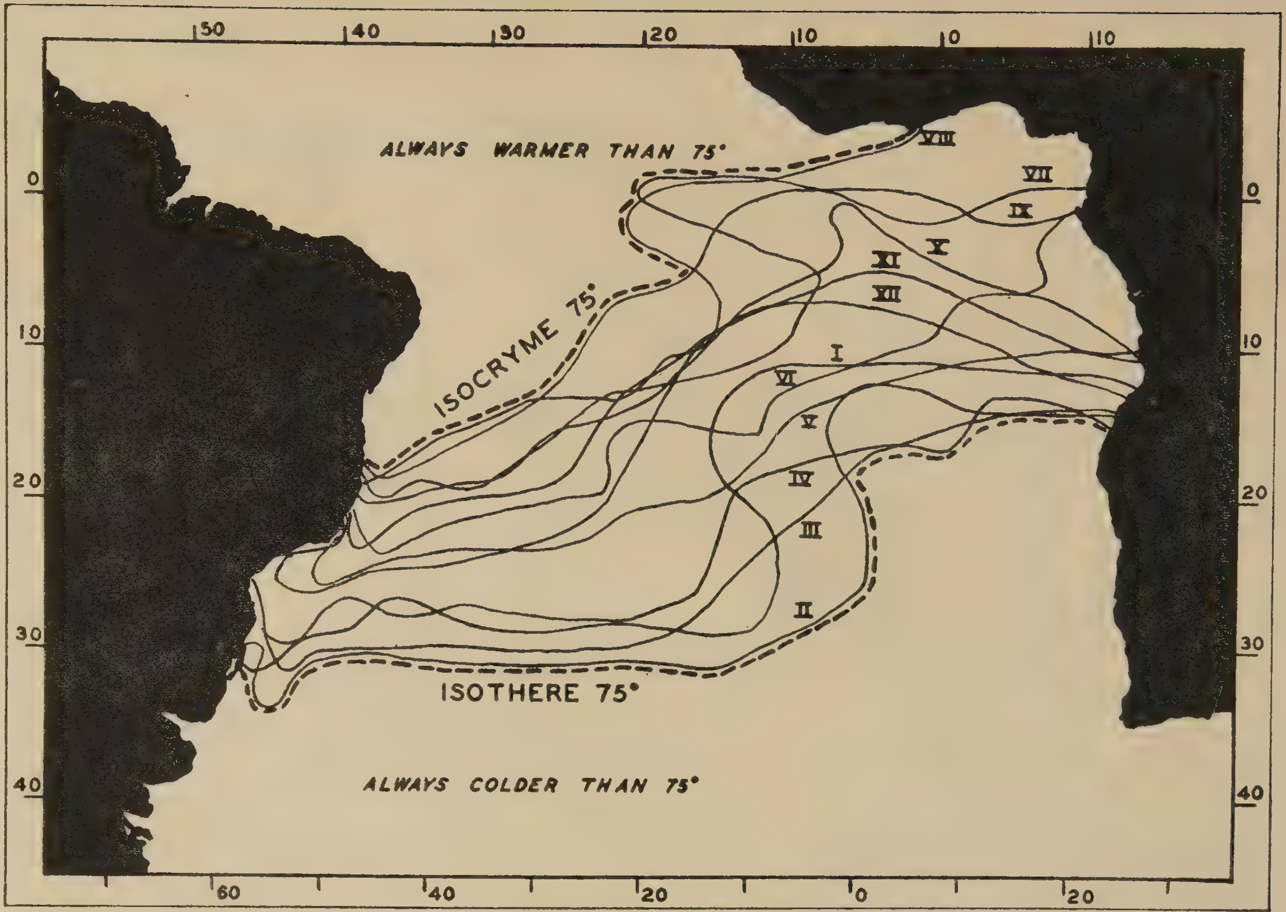

Figure 69. Illustration of the method of determining the courses of isotheres and isocrymes given in Plates I and II. The isotherms of 75° F. for each of the twelve months in the South Atlantic are superimposed on one chart. An area is thereby determined in which the surface water is sometimes more and sometimes less than 75°. The equatorward boundary of the area provides the isocryme, the isotherm of 75° at the time of greatest cooling, irrespective of the month in which this occurs. The poleward boundary of the area provides the isothere, or isotherm of maximum warming, in the same way.

tion of maximum monthly mean temperatures was determined from the poleward limits of all such areas and the distribution of minimum means from the equatorward limits.

Plates I and II thus give the maximum and minimum monthly mean temperatures irrespective of the months in which these occur. Their isotherms, in other words, connect points which warm up or cool down to the same extremes as measured in monthly mean temperatures. Such isotherms are known as ISOTHERES (equal warmth), and ISOCRYMES (equal coldness). Nominal calendar months being the basis of all calculations, rather than the warmest and coldest 30-day periods, the designations CALENDAR MONTH ISOTHERES and CALENDAR MONTH ISOCRYMES are appropriate.

It may be emphasized that Plates I and II give monthly means. Of course absolute maximum and minimum temperatures at any locality would be several degrees more extreme.

One exception to exact conformity with the Atlas has been made. Fuglister (1947) has reviewed more recently all of the data for the western North Atlantic and has prepared revised charts of that region. Plates I and II conform with his delineations of the maximum and minimum monthly means for the area (Fuglister, 1947: pl. 13, 14). On the whole, these do not differ significantly from the isotheres and isocrymes determinable from the Atlas alone.

Mercator projection has been used for Plates I and II instead of the sinusoidal equal-area projection of the Atlas. Hydrographic Office Chart 1262B served as the main base map. The arrangement whereby both the oceans and the continents are shown as unbroken masses appears to be the best suited to most general oceanographic and biogeographic purposes.

ACCURACY OF THE WORLD ATLAS AND OF PLATES I AND II

The Atlas, and the present charts of isotheres and isocrymes, appear to be reasonably reliable in the general patterns of temperature distribution shown. The highest sustained temperatures for the year round are found in the Indo-West Pacific Tropics, and in small sectors of the eastern Pacific and the western Atlantic Tropics, all of which have monthly means always in excess of 80° F. and mostly between 80° and 85°. The maximum temperatures, on the other hand, are found in the Persian Gulf, where monthly means exceeding 90° F. occur in summer, although winter monthly means in part of this area fall to about 60°. The greatest annual range, more than 40°, is found in the inner end of the Yellow Sea, where maximum means in excess of 75° and minimum means of less than 35° occur in the Gulf of Pohai.

Major upwellings and other large features of circulation in the surface waters are indicated by pockets, inflections and deviations of the individual isotherms. Not all irregularities of the isotherms are to be regarded as equally significant in this way, however, some resulting from peculiarities in the data or from procedural techniques such as charting the isotheres and isocrymes with as little smoothing as possible. It can be doubted, for instance, that the three warm spots enclosed by the isocrymes of 80° on the west coast of Central America are in reality as complex as the chart indicates.

Commentaries on the over-all accuracy of the Atlas are given by its compilers, and, indirectly, by Fuglister (1947). The former state that the delineation of isotherms for intervals smaller than 5° F. generally would give a false impression of the adequacy of the source data. Fuglister discusses the distortions introduced by the method used in compiling and reducing data, in which random numbers of observations for various years are averaged by months for one-degree quadrangles of latitude and longitude. Steep gradients tend to be spread horizontally in this technique, partly by use of the quadrangle as the smallest measure of area, partly because the positions of gradients may vary somewhat from time to time, and partly because of inaccurate fixes of observations.

Comparison of the charts with detailed local data for a number of points in Europe, America, and Africa shows that the Atlas information is only approximately correct for the most inshore waters. This, of course, is unavoidable, partly for the foregoing reasons and partly because local detail can not be charted on a world map of convenient scale. Caution is required, therefore, in using the present charts in biological investigations involving shore collections, or in similar applications.

Inadequacies of the source data of the Atlas, chiefly in higher latitudes, probably account for certain other limitations which should be noted. Interpolated isotherms are given in some cases and contribute portions of the isotheres and isocrymes of the mean ice limit, 35°, and 40° in Antarctic waters. Elsewhere, occasionally no isotherms are provided. For such reasons it has been impossible to chart the 55° isothere in the Sea of Okhotsk, the 35° isothere north of Bering Strait, and the blank portions of the mean ice limits. The delineations in the Arctic, particularly those for summer regarding the Siberian and Canadian coasts from the Kara Sea to Baffin Bay inclusive, must be taken with considerable reservations. The U. S. Hydrographic Office (1946) "Ice Atlas of the Northern Hemisphere" does not indicate that a majority of these coastlines are ice bound in the warmest months, as the World Atlas suggests, but does plot a large, persistent free ice field in western Baffin Bay which can not be reconciled with the course of the 35° and 40° isotheres there. These and other discrepancies are partly offset by the fact that there are great year-to-year variations around the average conditions in the Arctic, notably for ice distribution, and delineations of mean positions of isotherms there are at best of only provisional interest.

In preparing Plates I and II it has been found that a few isotherms in the Atlas do not join perfectly from one sector of the oceans to the next. The differences are seldom more than 2° of latitude, however, and are of no great consequence. Smoothed transitions across the overlaps have been used where necessary for the isotheres and isocrymes.

The collection of more extensive data will doubtless warrant eventual revision of at least portions of the thermal picture in Plates I and II. If judiciously used, nevertheless, the present charts are serviceable for most purposes to which they can be put. Over a year of testing, they have proved highly satisfactory for the analysis of biological distributions as carried out in this laboratory (Hutchins, 1947).

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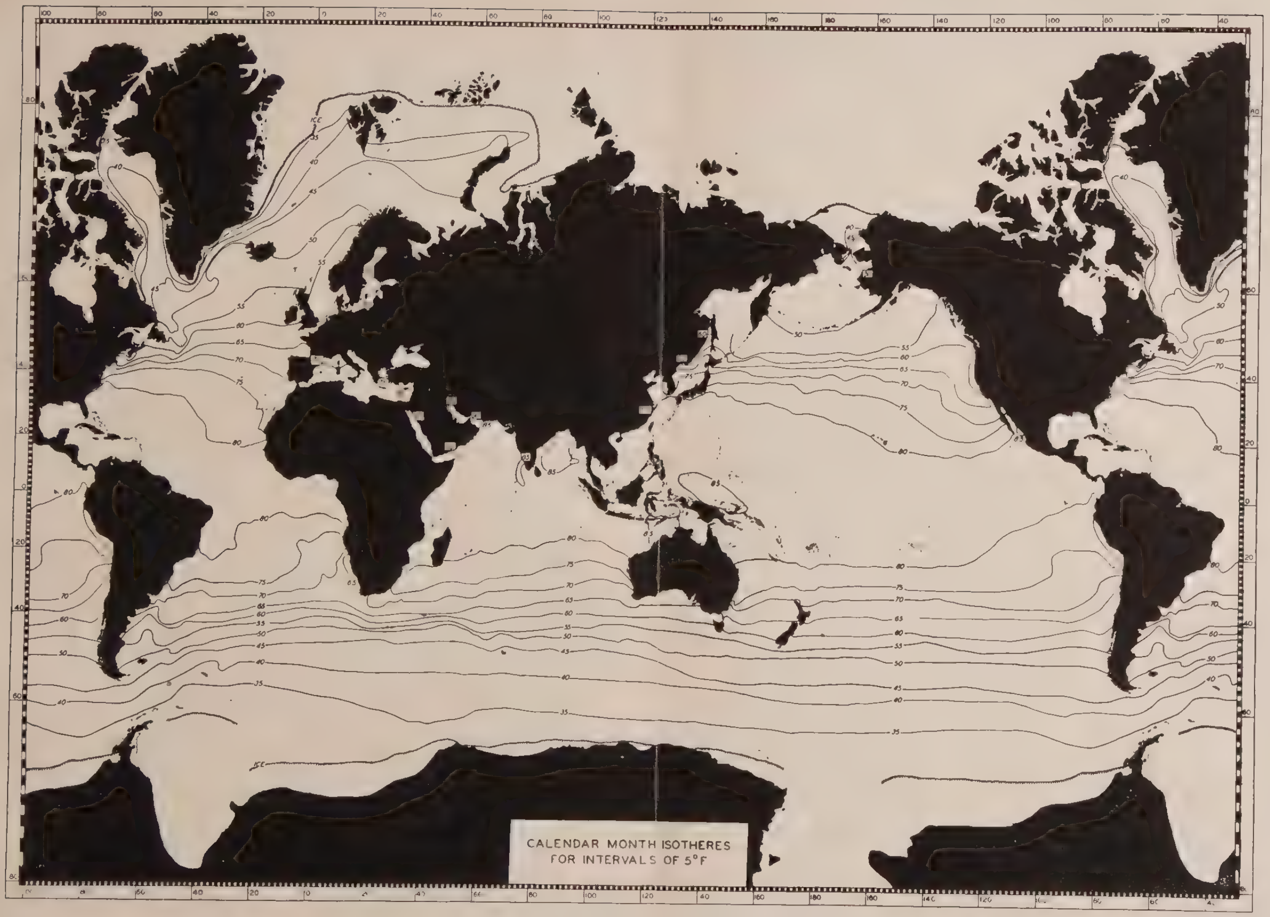

PLATE I

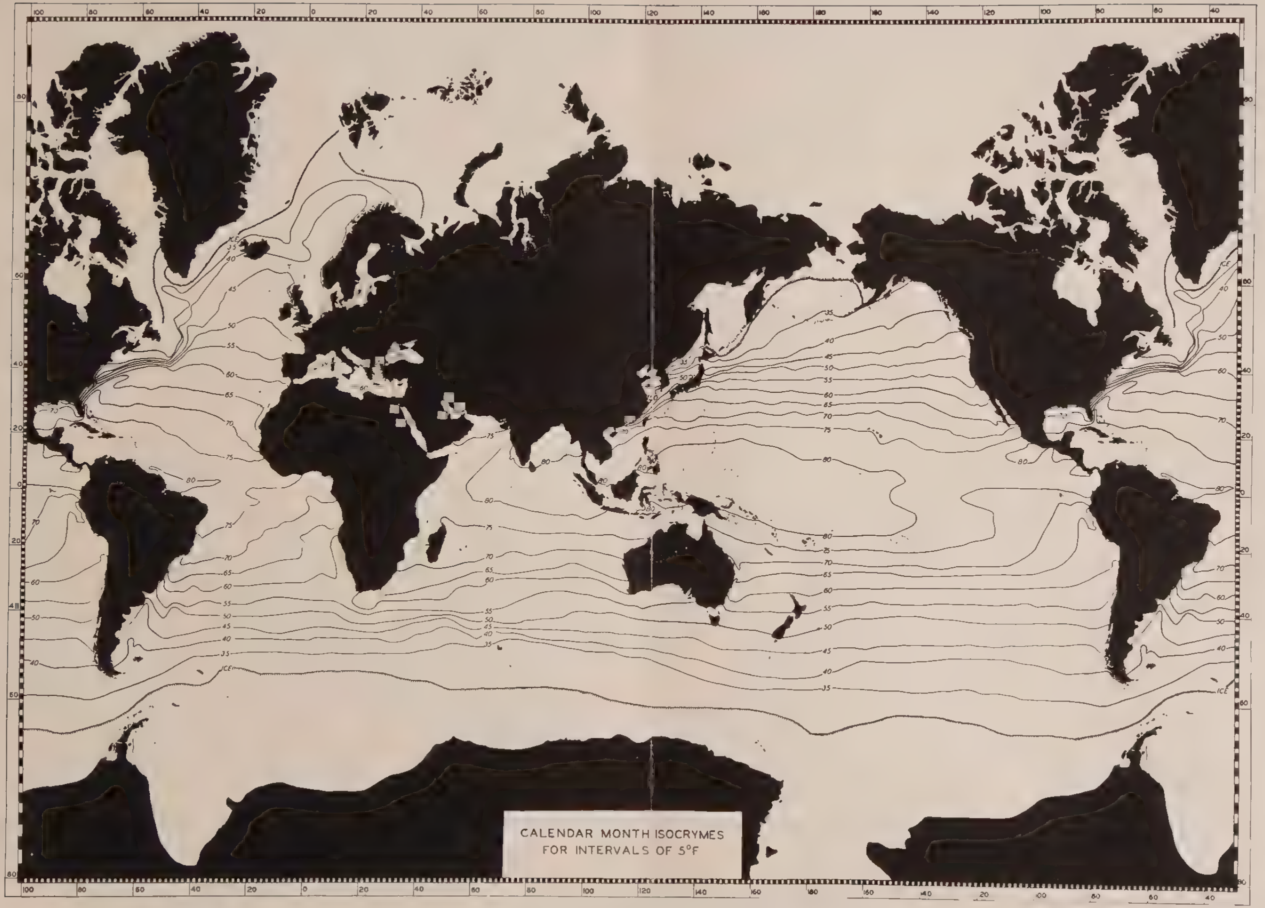
CALENDAR MONTH ISOCRYMES
FOR INTERVALS OF 5°F
ICE
35
40
45
50
55
60
65
70
75
80

PLATE II

Contribution No. 400

Reprinted from BIOLOGICAL BULLETIN, Vol. 93, No. 3, 240–249, December, 1947
Printed in U. S. A.

THE EFFECT OF ILLUMINATION AND STAGE OF TIDE ON THE ATTACHMENT OF BARNACLE CYPRIDS *

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The attachment of barnacle cyprids to exposed surfaces is influenced by the degree of illumination and the surface color. Cyprids of *Balanus amphitrite* and *Balanus improvisus* were found by Visscher (1927) to attach in greater numbers to dark or shadowed surfaces. McDougall (1943) noted this same behavior for the cyprids of *B. eburneus*. When exposed only at night, however, Pomerat and Reiner (1942) noted that *B. eburneus* attached to black, clear and opal glass in equal numbers. Twice as many barnacles attached to the black glass in natural day-night exposures. Gregg (1945) investigated the effect of contrasting dark surfaces against lighter general surroundings. He concluded that while no correlation could be established between the degree of contrast and the frequency of attachment, "shading" was suggested as acting as a stimulus to the attachment of the larvae of *B. eburneus* to opal glass collectors.

In the present investigation the rate of attachment of cyprids of *B. improvisus* during daylight and night exposures, and the effect of artificially illuminating the collecting surface at night were observed. The effect of the tide on the rate of attachment of cyprids was also studied. This work was carried out at the boat shed of the Beach Boat Slips Corporation in Biscayne Bay, Miami Beach, Florida.

METHODS

Four stations for sampling the barnacle cyprid population were established under and adjacent to a covered boat slip which extended 250 feet from the shore, the stations being at the outer end of the shed.

Stations A, B and C were control stations for comparison with Station D, which was illuminated at night. Stations A, D and B were spaced 55 feet apart, in that order in a north-south line paralleling the general flood and ebb movement of the tidal current. Station C was located 60 feet to the west of Station D. The conditions of natural and artificial illumination at each of these stations were as follows: In the daylight hours illumination at each of the four stations was nearly the same through the day. The intensity at each location depended on the proximity of the shadow of the shed. At Station A, daylight illumination was skylight; at Station B, the collector swung in and out of the sun and shadow of the shed with the phase

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* Contribution No. 400 from the Woods Hole Oceanographic Institution. The observations were made during an investigation by the Woods Hole Oceanographic Institution under contract with the Bureau of Ships, Navy Department, which has given permission for their publication. The opinions presented here are those of the author and do not necessarily reflect the official opinion of the Navy Department or naval service at large. The author is indebted to Dr. B. H. Ketchum, Dr. L. W. Hutchins and Dr. A. C. Redfield for helpful advice and criticism and to Mr. Alexander C. Frue for assistance in making the observations.

of the tide; and Station C was in full sunlight, whereas Station D was under the shed roof and in the full shadow. At night, Station D was artificially illuminated, while Stations A, B and C were in darkness.

Collecting units consisting of four pieces of black glass (500 sq. cm. collecting area) were suspended from a float. The surface panel was horizontal while the others, at depths of 2, 6 and 10 feet, were hung in a vertical position. The 10-foot level was just above the bottom at low tide and three feet higher at high tide.

The periods of collection, day and night, were eleven hours each, from 7:30 A.M.–6:30 P.M., and 7:30 P.M.–6:30 A.M. The eleven-hour exposure permitted no significant overlapping period of dark to light or light to dark when the collectors were in the sea. The one-hour interval between exposures permitted counting, cleaning and reimmersing of the collection units.

TABLE I

Numbers of cyprids attaching during consecutive night and day periods of eleven hours each at three stations. The figures are the sum of the collections on four panels of 500 sq. cm. area each, hung at different depths.

Cyprid attachment night			Cyprid attachment day			Average	
Stations			Stations			Night	Day
A	B	C	A	B	C		
*394	205	306	403	614	784	302	600
418	279	272	386	897	997	323	760
463	534	778	1361	1392	2018	592	1590
434	768	497	701	666	1147	566	838
296	160	483				313	
**444	533	432	2352	1149	3564	470	2355
391	446	541	636	569	1829	459	1011
255	201	479	432	881	1092	312	802
219	168	240	676	564	1581	209	940
114	99	101				105	

* February 11, 1946–February 16, 1946. ** February 26, 1946–March 3, 1946.

Although the source of illumination at Station D remained fixed while the collector unit which hung below it rose and fell with the tide, an average distance of 5 feet from the lights to the water surface was used in calculating the value of incident illumination at the water surface and at the 10-foot depth. The incident illumination five feet from the lights was measured by a direct reading photometer and that at the 10-foot level calculated by using an absorption factor for the local waters determined with an underwater photometer.

The study of cypric attachment relative to stage and direction of the tide was made by counting the cyprids attaching during intervals of two hours throughout a tidal cycle in daylight hours only. The collecting units were the same as those employed in the illumination experiments.

Diurnal Variation in Cyprid Attachment

Observations on five successive nights and four intervening days in two separate series indicated that many more cyprids settled during the period of daylight, as shown in Table I. In the first set of observations, the ratio of the average of all the day collections to the average of the corresponding night collections indicated an increase of 2.1 times the number of cyprids attaching in daylight, while in the second series the ratio of day to night attachments was 3.5.

It is of interest to note that in the first set of collections when the cyprid density, as shown by total attachment day and night, was lower than the second set of collections there are examples of day collections being nearly of the same magnitude or even slightly less than the night attachments. This condition was found only at Stations A and B which were wholly or partially shaded from direct sunlight during the daylight hours. A partial explanation of the relatively high night attachments of the first set of collections may be due to the fact that these were made under the full of the moon whereas the second set were made in the dark of the moon. However, when the cyprid density was high, as during the second set of observations, no discrepancies from the diurnal fluctuation in attachment were noted. The maximum differences between night and day attachments were always found at Station C which had the maximum difference in illumination.

Vertical Distribution of Cyprid Attachment

The vertical distribution of barnacle cyprids at Stations A, B and C showed no consistent pattern which would suggest dependence on any particular controlling factor. In the first set of collections, shown in Figure 1, the maximum numbers at Station A, both day and night, were found at the 2-foot level. At Station B, all the day collections showed cyprid peaks at the 6-foot level, whereas, at night, attachment was nearly uniform between the 2-foot level and the bottom, except for one observation. At Station C, the day collections resulted in maxima at the 2-foot level on three occasions and a 6-foot maximum on one occasion.

The second series of vertical samplings, as shown in Figure 2, were made at a period of higher cyprid density which resulted in collections of considerable magnitude for several of the eleven-hour periods. However, no consistent pattern of vertical distribution was apparent.

This erratic distribution of cyprids, both vertically and in comparison of stations, is of particular interest, in view of the relatively close proximity of the collecting units. The apparent random attachment of cyprids to the collecting units is probably due to a nonuniform distribution of cyprids in the water. Since the number of cyprids attaching does not decrease with depth, it is apparent that intensity of illumination does not control vertical distribution.

Effect of Artificial Illumination on Cyprid Attachment

The normal diurnal cycle, with lower attachment numbers at night, was abolished by the use of artificial illumination at night at Station D. The cyprid attachments at night under artificial illumination at Station D were greater than the daylight counts at this location and were nearly as large as the daytime collections at Station C where the intensity of daylight illumination was greatest. As shown in

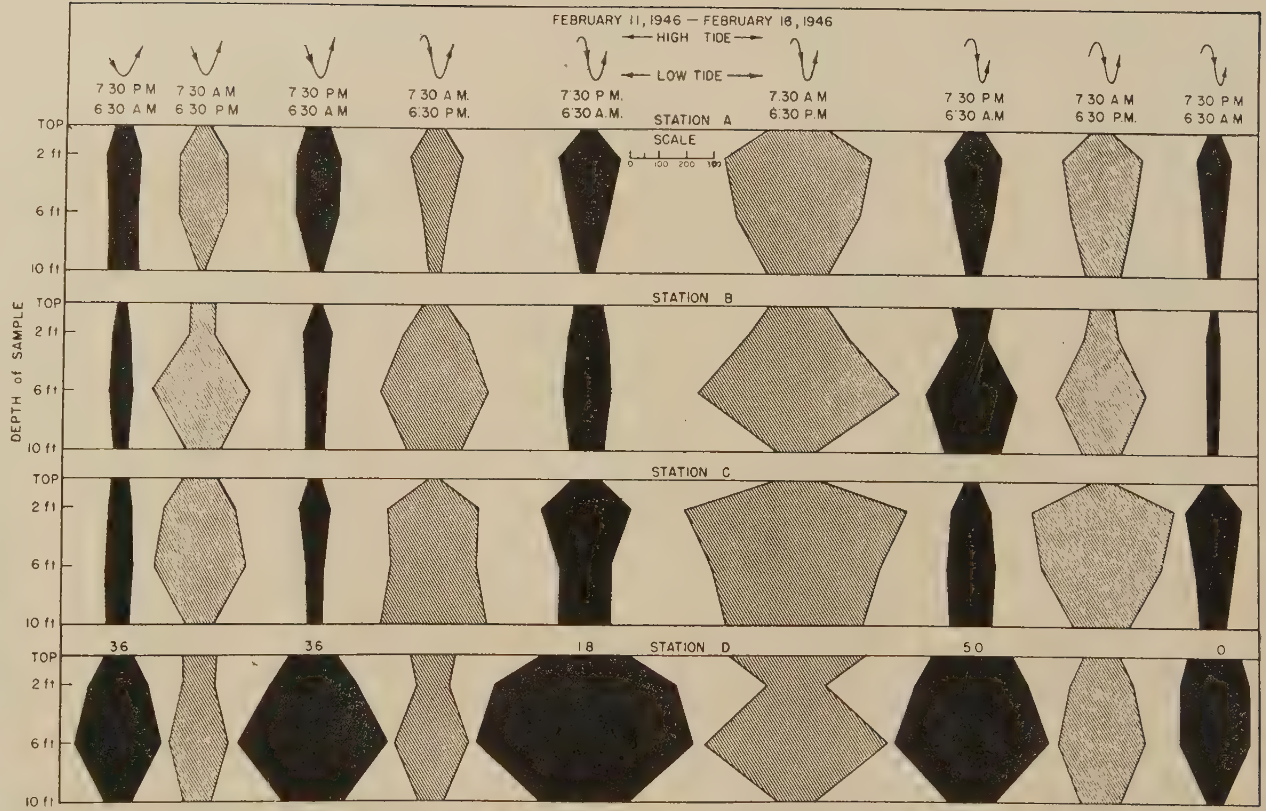

Figure 1. Vertical distribution of cyprids at four stations as collected in eleven-hour periods, February 11, 1946–February 16, 1946. The tidal curves at the top of the figure represent the stages of the tide in which the collection took place. The numbers over the night collections of Station D are the illumination values in footcandles at the water surface used for that exposure.

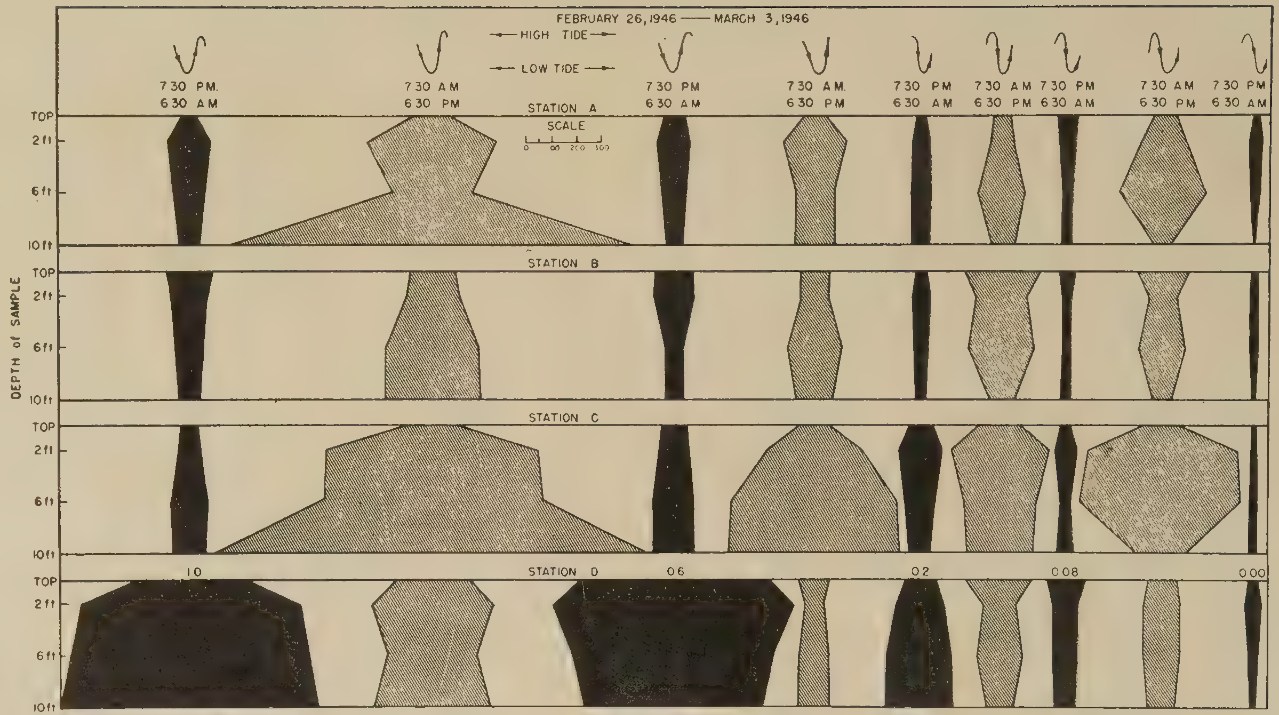

FIGURE 2. Vertical distribution of cyprids at four stations as collected in eleven-hour periods, February 26, 1946–March 3, 1946. The tidal curves at the top of the figure represent the stages of the tide in which the collection took place. The numbers over the night collections of Station D are the illumination values in footcandles at the water surface used for that exposure.

Figures 1 and 2, artificial illumination, however, had little if any effect on vertical distribution of the cyprids.

In order to determine the intensity of illumination necessary to increase the cyprid attachments at night, the illumination over the collectors at Station D was systematically changed. In the first series, the incident illumination at the water surface was varied from 36–1.0 footcandles, and in the second experiment, from 1.0–0.00 footcandles. The variations in vertical distribution at each station, which are apparently due to other factors, have been smoothed by totaling the cyprid accu-

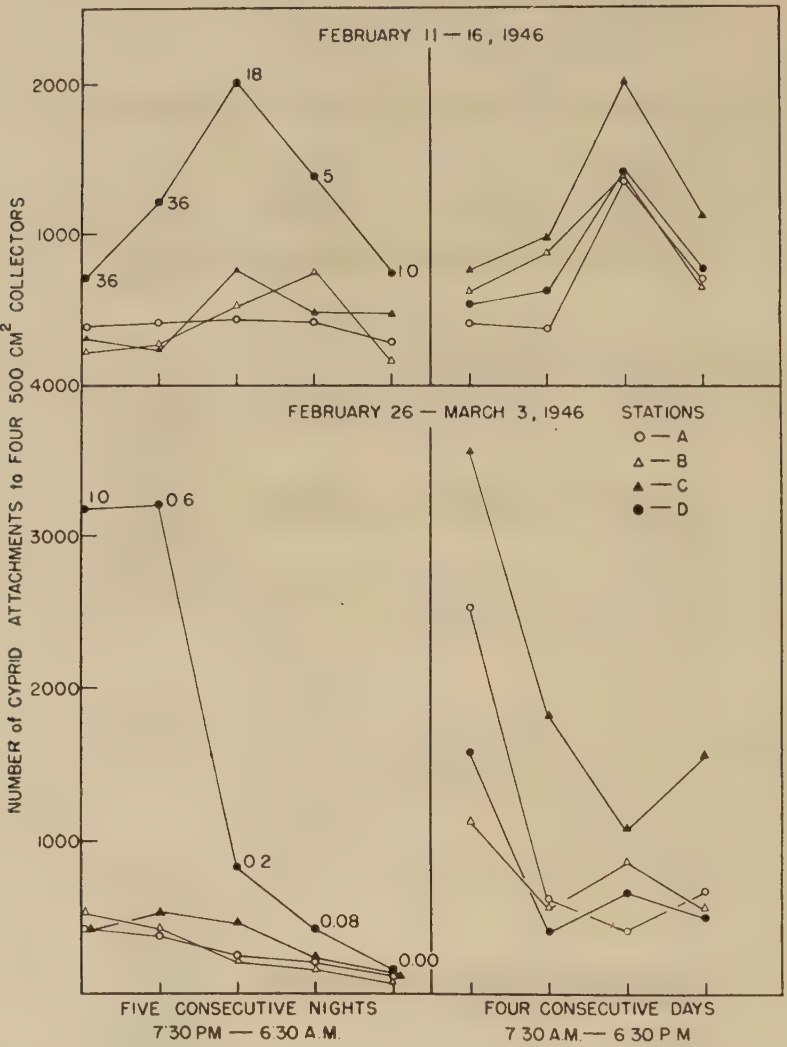

Figure 3. Total cyprid attachment for the eleven-hour collection periods at each station. The numbers plotted with Station D, night collections, are the values in footcandles at the water surface of the artificial illumination employed.

mulations from each of the four glass collectors. This figure then represents the catch from the cyprid population of a vertical column of water. As shown in Figure 3, the illumination of the collectors at Station D resulted in a two to sevenfold increase in numbers of cyprids attaching over those found on the control surfaces. The daily variation in cyprid numbers attaching at night to the illuminated collectors of Station D resembled more nearly the daily fluctuation in cyprid density as found on the daylight collections of Station C. Although the night collections of Station D paralleled the cyprid density fluctuations as found at the unilluminated stations, they were of course several times greater in magnitude. This result was obtained within the limits of illumination of 36 to .08 footcandles at the water surface. On the final night exposure of the second series, when Station D was not illuminated, its cyprid collection was still slightly greater than the other three stations. However, this difference is probably within the normal variation. During the day the collections at Station D were of the same magnitude as at A and B and considerably less than those at C.

TABLE II

Numbers of cyprids attaching in eleven hours at night at the 10-foot depth at Station D as related to quantity of artificial illumination and in comparison with the simultaneous attachment at Stations A, B and C.

Value of illumination at D at 10-foot depth (footcandles)	Stations				$\frac{D}{1/3(A+B+C)}$
	A	B	C	D	
*5.2	110	45	87	102	1.3
5.2	38	71	56	219	4.0
2.5	45	117	184	318	2.8
.71	42	206	136	169	1.3
.14	44	34	90	64	1.1
** .14	78	92	135	1005	9.9
.09	59	71	158	710	7.4
.03	65	37	81	257	4.2
.001	38	44	66	77	1.6
.000	7	15	33	21	1.1

* Five consecutive nights—February 11, 1946–February 16, 1946.
** Five consecutive nights—February 26, 1946–March 3, 1946.

The artificial illumination, even at the 10-foot depth, consistently increased the number of cyprids attaching to the collecting surface of Station D in comparison with the control stations, as shown in Table II. The ratio of the attachment at Station D to the averages of Stations A, B and C indicates the degree of change in attachment due to illumination. The greatest differences between the illuminated collectors and controls occurred on the second and third nights of the first experiment when cyprid attachment was at a maximum. In the second set of exposures, when cyprid density was high, all the collections at the 10-foot level of Station D, even though the illumination was very low, were invariably greater than all the controls.

As indicated above, the illumination of the water surrounding the collectors was varied systematically to determine the minimum value to which the cyprid would respond. When the cyprid density was high, thus providing more organisms which would by random selection be subjected to the contrast of luminous zone and dark area, the greatest change in cyprid attachment occurred when the illumination of the water surface was changed from 0.6 to 0.2 footcandle. At 0.6 footcandle and greater intensities, the difference in cyprid settling, in comparison to the controls, was sevenfold, while at 0.2 footcandle and less, the increase over the control collectors was only twofold. However, at illumination as low as .03 footcandle, increases in attachment over control collectors were still considerable.

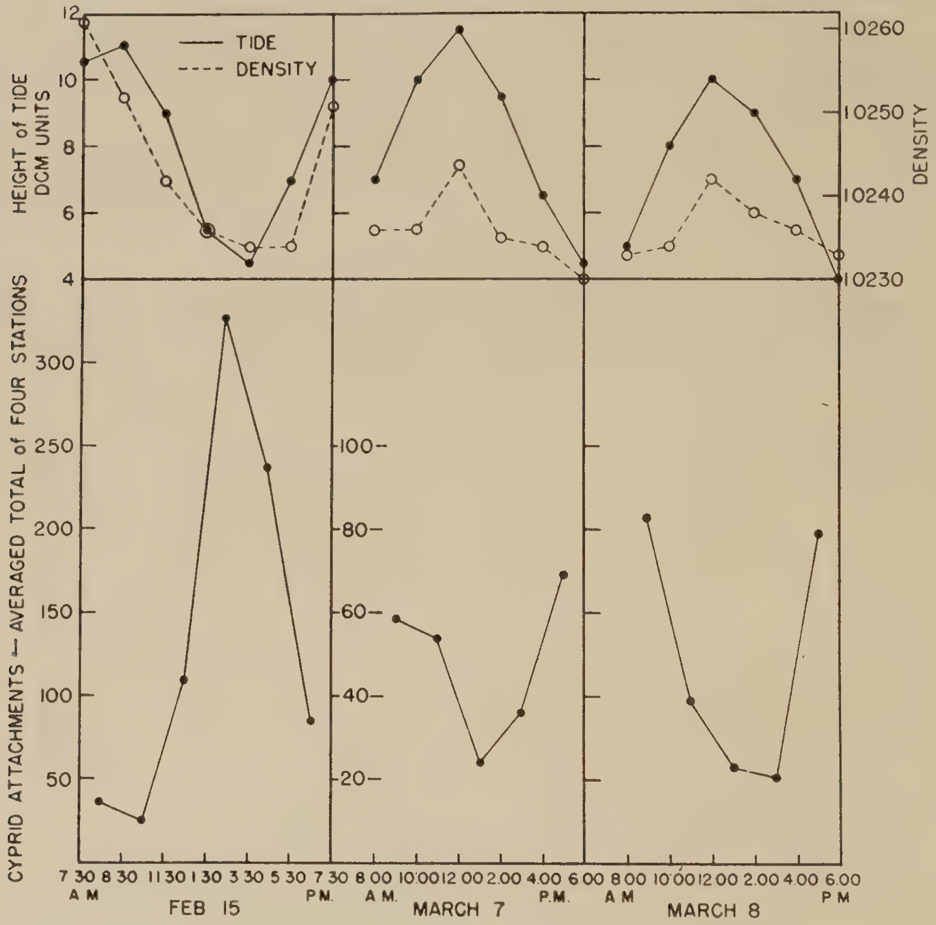

FIGURE 4. Bi-hourly cyprid attachment at each station totaled from the four collecting surfaces. The height of tide is noted in decimeter units. February 15, March 7 and 8, 1946.

Previous investigations (Visscher, 1927; Pomerat and Reiner, 1942; and McDougall, 1943) showed that the barnacle cyprid attaches in daylight in greater numbers to dark surfaces than to light surfaces. At night, as is to be expected, there is no distinction between the two colors. In this investigation illumination of dark collecting surfaces at night increased attachment. One effect of illumination is to increase the contrast between the dark surfaces and the surrounding water. In waters with considerable suspended material, as usually found in harbors and estuaries, a beam of light is markedly scattered, producing a general illumination in the water. A piece of black glass suspended in these waters under a source of illumination was discernible to the observer as a black area surrounded by brighter water. When the water appears brighter than the collecting surface, at night because of artificial illumination, or during daylight, the cyprids may be attracted to the darker area by some negative phototropic response and may accumulate there in greater numbers than would result from chance encounters. In contrast, in the absence of light at night, the numbers of cyprids attaching may depend solely on chance encounters with the collecting surface, and are consequently lower than during periods of illumination.

Effect of Stage of Tide

On collectors exposed through the day and examined at two-hour intervals, the maximum numbers of cyprids attached during the low-tide period as shown in Figure 4. This was found whether the low tide occurred at midday, in the early morning, or late afternoon. As in the case of the longer exposures, there was no indication that the distribution of cyprids on the panels was influenced by the depth at which they were hung.

At the location of this experiment, the ebbing tide brings to the boatshed water which is isolated within the bay. It is replaced at high tide with oceanic water entering the bay on the flood. This is shown by the change in density accompanying the tidal cycle. The isolation of the bay water permits development of a large cyprid population, since few of the plankton stages are lost into the ocean prior to metamorphosis to the cyprid stage. At the low-tide period, the sampling location was occupied by the bay water with high cyprid content, and this apparently accounts for the greater attachment at that time. The high attachment at low tide cannot depend upon the lessened flow at that time, since a similar slack water occurs at high tide when the attachment is minimal.

Summary

1. The cyprid larvae of *Balanus improvisus* were found to settle in a diurnal rhythm with maximum numbers attaching during daylight hours.

2. No consistent pattern of vertical distribution of the cyprids was found.

3. The normal diurnal cycle in rate of attachment of barnacle cyprids was nullified by the use of artificial illumination over the collecting surfaces at night.

4. The magnitude of the cyprid collection on the artificially illuminated surfaces was equal to the collection on the sun-illuminated surfaces in daylight.

5. The intensity of artificial light necessary to produce large cyprid attachments at night was of an order as low as 1 footcandle at the water surface.

6. No correlation was found between the quantity of artificial light at night and the numbers of cyprids attached.

7. The highest rate of cyprid attachment relative to the phase of the tide was found to occur when the waters of upper Biscayne Bay were sampled at the collecting station. This body of water reached the sampling station at low tide and was characterized by a high cyprid population.

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Contribution No. 414

MEASUREMENTS OF PRODUCTION IN FERTILIZED SALT-WATER[1, 2]

By

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The present paper describes some results of several exploratory experiments made at the Woods Hole Oceanographic Institution in connection with a proposed study of organic production in salt waters. An attempt is made to relate the viewpoint of the present paper to the more outstanding aims of fertilization work. Aside from practical matters of aquiculture, addition of nutrients to water is a valuable tool for studying what has been called food-chain dynamics. Briefly stated, the object of the described experiments was to determine immediate effects of fertilization upon the vital activities of the phytoplankton.

Of the four experiments to be mentioned, two were performed in an outdoor concrete tank built in Woods Hole for the purpose, the others in Rand's Harbor near Woods Hole. The tank at Woods Hole is made of high quality concrete and it is divided down the middle by a concrete partition, making two separate compartments, each being 5.70 x 2.74 x 1.53 meters. Notches in the wall permit insertion of heavy wooden partitions which divide each compartment into four equal sections. For purposes of these experiments, one undivided compartment was used. The concrete was thoroughly washed after setting and was leached with sea water for several weeks before use. No untoward effects of the concrete on the water were observed during the experiments; *e. g.*, the pH did not change during soaking with sea water after the initial washing, although it increased as expected during heavy plankton growth.

Rand's Harbor is an irregularly Y-shaped embayment of Buzzards Bay about ten miles from Woods Hole. The length of the larger branch is about 375 meters, of the smaller branch 250 meters, and of the foot roughly 125 meters. The end of each branch away from the seaward connection is a somewhat enlarged basin. The deepest part of the small branch is about 3.5 meters at high tide and of the large

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[1] Contribution No. 414 from the Woods Hole Oceanographic Institution.

[2] One of a series of papers presented at a symposium, "Fertilization of Aquatic Areas," sponsored by the Limnological Society of America at Boston, 1946.

branch about 5 meters. The extreme range of tide is about 1.5 meters. The opening to Buzzards Bay is about 5 meters wide and 1.8 meters deep at high tide. Rand's Harbor was under intensive investigation between March 1 and September 1, 1946. On two occasions fertilizer was added to the smaller arm.

The work discussed here is part of a co-operative project initiated and supervised by Dr. George L. Clarke. The counts of tank plankton were made by Miss Mary Goffin, of the Rand's Harbor plankton by Dr. S. P. Chu. Miss Marion Hawes furnished much assistance in making chemical determinations. Other help is acknowledged subsequently.

METHODS

Oxygen. Oxygen was determined by the Winkler method as described by Theroux (1943). The concentration of oxygen is expressed as milligram-atoms per liter as recommended by the International Association of Physical Oceanography (Sverdrup, *at al.*, 1942: table 34). Since oxygen is almost invariably given by limnologists as milligrams per liter, this mode of expression is also recorded in order to make values more readily comprehensible to all readers. The definite advantage of the former method is that the figure is proportional to the number of oxygen atoms rather than to the mass, which makes intercomparison of amounts of various elements easier in the light of definite chemical reactions and compounds. This is particularly useful with oxygen when considering photosynthetic equations and the amounts of carbon dioxide and carbohydrates involved. One mg. of O_2 = 0.0625 mg.-at.; one mg.-at. is 16 mg.

Photosynthetic Oxygen Production. The technique for measuring rate of photosynthesis is familiar, having been used by Manning and Juday (1941), Juday, Blair and Wilda (1943), Riley (1943), and others. In the present work, round clear glass bottles, with a volume of about 200 ml., were filled from the tank with raw water that was strained through stramin in order to remove large pieces of debris which might have been present. For each experiment four bottles were so filled, two of which were wrapped with several layers of black cloth and two left uncovered;[3] all four bottles were suspended in the middle of the tank at mid-depth in such a way that they were exposed freely to the light. Initial oxygen, phosphate, and plankton concentration were measured. At the end of two or four days the bottles were retrieved. Oxygen was determined on one pair of bottles, light and dark, phosphate and plankton on the other pair. The mean rates of change of oxygen and phosphate were then calculated by dividing the change from initial conditions by the time of exposure. The rate of increase of oxygen in the light bottle represents the rate of formation of oxygen by photosynthesis less the rate of consumption by respiration. The latter is measured by the change in the dark bottle. Subtracting the rate in the dark bottle (a negative quantity) from the rate in the light bottle gives the total mean rate of production.

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[3] Hereafter referred to as "dark" and "light" bottles.

The results of such determinations may be distorted by a number of factors which partially counterbalance each other. The phytoplankton started dying in the dark bottles while increasing in the light in these experiments. It might be thought, therefore, that the dark bottles did not sufficiently estimate the rate of respiration; however, it is known that bacteria and nonphotosynthetic protozoa multiply more rapidly in the dark bottles than in the light, and their respiration makes up for the loss of plankton, at least in part. The errors may be partly minimized by keeping the time of exposure as short as possible; yet the time must be long enough that the change in oxygen concentration is significantly larger than the error of determination. It is also necessary that the time of exposure of the bottle be short enough that the supply of carbon dioxide is not depleted. In these experiments, using sea water, this is unlikely to happen. Concordant results were given by three determinations, two covering two days each, which coincided with a longer four-day determination.

Hydrogen-ion Activity. The pH was determined with a Hellige colorimeter and the results corrected for salt error.

Phosphate. Phosphate was determined by the Atkins-Denigès molybdate method except that 1 ml. of solution was used instead of 2 ml. (Wattenberg, 1937). The intensity of the blue color was measured with a Klett photoelectric colorimeter which had been standardized with solutions of known phosphate content. Klett no. 66 filter and a 4 cm. cell were used. All measurements were corrected for salinity. Since the intensity of the blue color changes with time, all determinations were made during the period between five and fifteen minutes after the addition of reagents. The concentration is expressed as microgram-atoms of phosphate phosphorus per liter as recommended by The International Association of Physical Oceanography (Sverdrup, *et al.*, 1942: table 34). One μg.-at. of phosphate phosphorus is equivalent to 30.98 μg. of phosphate phosphorus, or 94.95 μg. of phosphate.

Chlorophyll. Two-liter samples of sea water were filtered in a modified Seitz filter through Whatman no. 42 paper on which had been deposited a layer of barium sulfate as described by Redfield, Smith and

Ketchum (1937: 423). One liter of water was used when much plankton was present. The entire filter medium was then ground with Merck reagent sea sand in a mortar and extracted with 80% acetone in the dark for fifteen minutes. The extraction mixture was filtered through a sintered glass filter and the filtrate read with a Klett photoelectric colorimeter.[4]

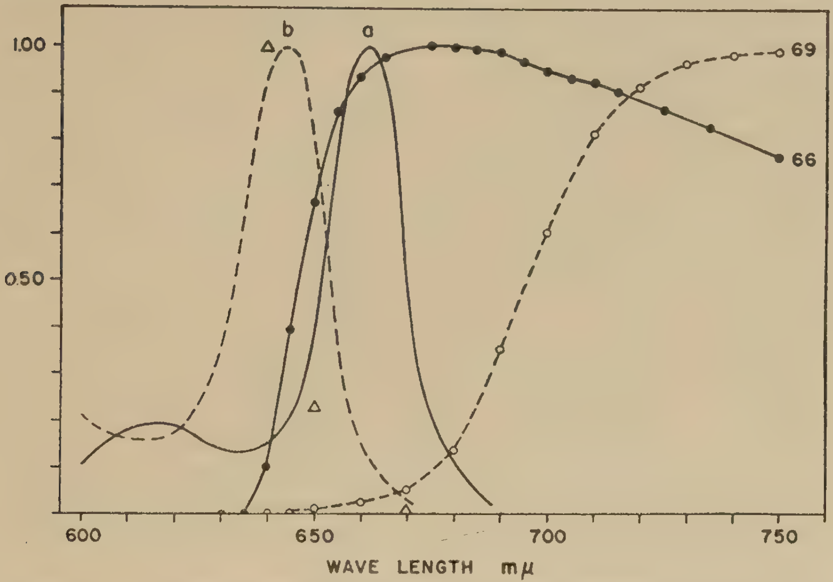

Figure 55. Absorption of light by chlorophylls *a* and *b* and chlorofucine (triangles) in acetone and transmission of light by Klett filters no. 66 and no. 69. For purposes of comparison, maximum transmission or absorption has been taken as 1.0 with all other values expressed as fractions of the maximum. Data for chlorophylls *a* and *b*. from Harris and Zscheile (1943), are relative absorptions (= log I_0/I). Data for chlorofucine from Strain and Manning (1942). Data for transmission by the filters are simply the percentages of peak transmission at the given wavelengths.

Readings were always taken with Klett filters no. 66 and no. 69, since at the time it was uncertain which was most suitable. Subsequently the authors determined the transmission spectrum of the filters using a Beckman spectrophotometer. The results of these measurements are compared with the absorption spectra of chlorophylls *a* and *b* in Fig. 55. For the filters, the maximum percentage transmission was taken as 1, and the transmissions at various wavelengths calculated as fractions of the maximum. The curves for chlorophylls are derived from graphs published by Harris and Zscheile (1943). The maximum relative absorption in the red was similarly taken as 1 and relative absorptions at the various wavelengths expressed as fractions of the maximum. The graph indicates that Filter no. 66 is the better for measuring concentration of chlorophyll *a*, although there could be some interference from chlorophyll *b*. The calibration data showed that Filter no. 69 was relatively insensitive to both chlorophylls. There is no chlorophyll *b* in the diatoms which made up most of the plankton in this work. Chlorofucin may also interfere to some extent, but it is felt that this is a minor effect. Chlorofucin evidently is a normal component of diatoms (Strain and Manning, 1938).

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[4] The instrument had been calibrated by Dr. Harold Haskin, using samples of pure chlorophylls *a* and *b* kindly supplied by Dr. Richard Goodwin of Connecticut College.

Plankton. A 100 ml. sample of water was treated with six drops of Lugol's solution and allowed to settle overnight. The supernatant water was carefully poured off. The numbers of organisms were recorded, usually to genera, although in some cases species could be recorded and in other cases only families. The counting was done by the method described by Chu (1942). The period of settling should be much longer when small flagellates are present, but with the plankton present in the tanks, this period gave a sufficiently accurate estimation of the important elements of the phytoplankton.

In order to estimate somewhat better the actual amount of material present, the volume of each type of organism was estimated from mean size and the total volume of phytoplankton present calculated. Much reliance should not be placed on these volumes, since the mean sizes used are not precise.

RESULTS

Experiment 1

Only one of the experiments is to be described at length here. On the morning of August 20, 1946, the concrete tank at Woods Hole was filled with 15,000 l. of sea water pumped in from the adjacent harbor. The water was passed through a very large net of no. 10 bolting silk to remove the copepods and fish, reducing the larger zooplankton to a negligible number. Bottles were immediately filled for photosynthesis determination, using the raw sea water. Thereupon 100.5 g. of Reagent $NaNO_3$ dissolved in a small quantity of distilled water was poured into the tank and the water vigorously stirred to assure complete mixing. A second set of bottles was filled for another photosynthesis determination, using this nitrate fertilized water. Finally, 10.2 g. of Reagent KH_2PO_4 was similarly added, the tank stirred, and another set of bottles filled. Thus three determinations were run concurrently for four days: one without fertilizer to serve as control (Fig. 56a), one with nitrate (Fig. 56*b*), and one with both nitrate and phosphate (Fig. 56*c*). Since only one tank was available at the time, a full control (a tank full of unfertilized water) was not possible. The amount of phosphate added was calculated to increase the concentration by 5.0 mg.-at. of phosphorus per liter. The initial concentration in the water was 0.93, and that measured after fertilization 5.82. The nitrate added was calculated to make the proportion of nitrogen to phosphorous 7.1 by weight or 15.6 by number of atoms. This is the average ratio in marine plankton (Sverdrup, *et al.*, 1942: 236).

Each day during the thirteen day period of the experiment, after the water was mixed by stirring, measurements were made of phosphate, temperature and pH. Salinity was measured on the first day and on several subsequent days. On some days measurements were made again in the afternoon; this was always true of temperature and pH, frequently of phosphate. The water temperature during the experiment varied between 20° and 22° C. Every second day chlorophyll was determined, and bottles were filled for starting a new photosynthesis determination. During the first part of the period these ran for four days, but starting on August 26 additional determinations were started which ran for but two days. Thus, during the latter part of the period two experiments were run concurrently. The plan is shown schematically in Fig. 56, which also serves as key to other figures, where values for mean rates determined are plotted at the midpoint of the experimental periods.

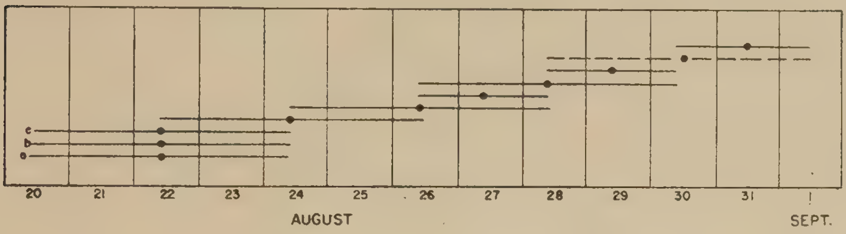

Figure 56. Plan of Experiment 1 in tank from August 20 to September 1, 1946. The horizontal lines represent the duration of exposure of bottles in determination of rates of photosynthesis. In subsequent figures, data are plotted at the midpoints of the periods. Three determinations were started on August 20 as described in text. The determination of photosynthesis during the period August 28–September 1 was unsatisfactory.

Changes in the standing crop of living phytoplankton in the tank are shown in Figs. 57 and 58 and of phosphate and oxygen in Fig. 59. At the beginning of the experiment the principal organisms in the

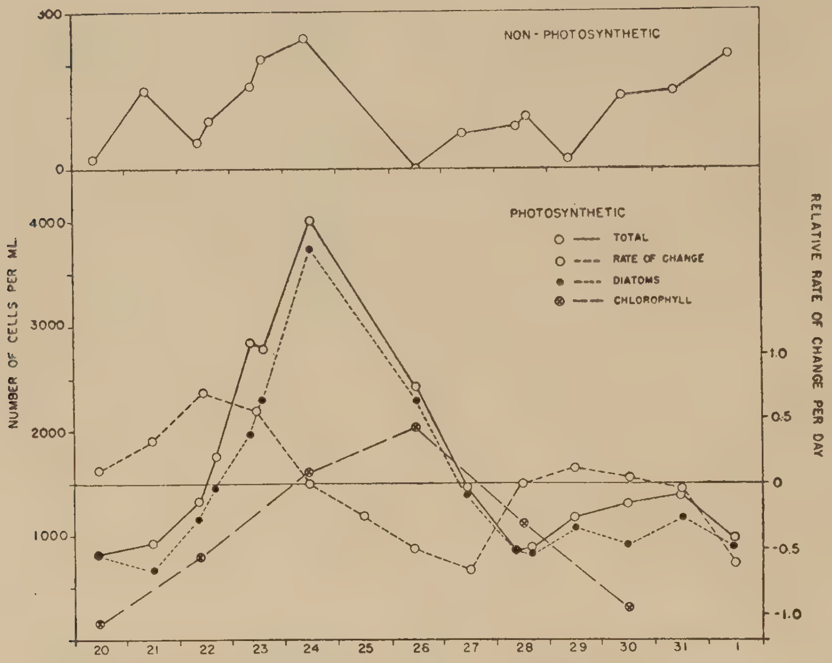

Figure 57. Numbers of phytoplankton cells (photosynthetic) and of nonphotosynthetic unicellular organisms during Experiment 1. Chlorophyll as mgm./1. × 100 is read on left scale.

phytoplankton were the diatoms *Corethron* and *Leptocylindricus*. By the end of the experimental period *Leptocylindricus* had disappeared and the diatom *Amphiprora* had become the dominant form. In addition, the dinoflagellate *Protocentrum micans* increased in numbers until August 29, after which it suffered a sharp decline. The population, as measured by number of cells, grew rapidly, reaching a peak on August 24 and then declining as rapidly. The rapidity of fall is notable but is nearly matched by some of Riley's (1943) experiments with *Nitzschia*. A smaller peak occurred on August 30. The relative rate of change of size of the population was calculated as follows: a smooth curve was drawn through the points, and from this was read the number of organisms present at the beginning of each day. The daily change, increase or decrease, was divided by the mean number present during the day. The value for August 20 was adjusted to allow for the fact that the experiment was started during the morning. The result of the calculations shows that after a period of acceleration the population was most actively growing on August 22, although the maximum

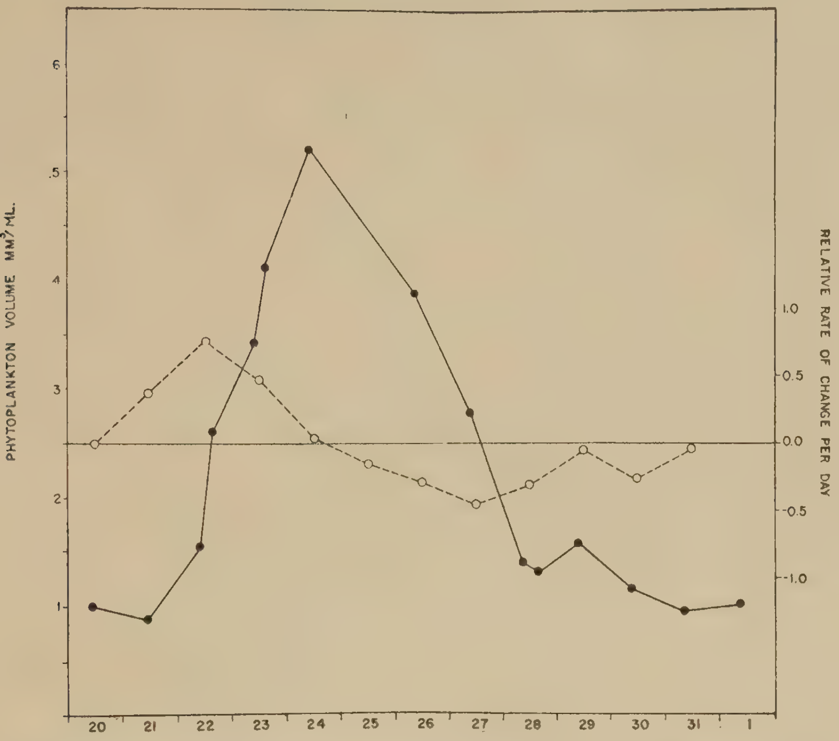

Figure 58. Phytoplankton volume during Experiment 1 as mm³ of cells per milliliter of water. Relative rate of change shown by broken line.

number was not achieved for two more days. The second peak was the result of considerably slower multiplication. The relative rate of population growth is the reproductive rate less the death rate. Since predation may be regarded as negligible here, the figures, during periods of increase, approximate the reproductive rates.

The initial stages of growth in volume of the phytoplankton were very similar, although the later stages were different (Fig. 58). The relative insignificance of the second peak, which occurred later than the peak in numbers, is accounted for by the fact that there were fewer of the largest diatoms, *Corethron* and *Rhizosolenia;* this difference reduced the volume more than the numbers of cells.

The chlorophyll content increased rather less rapidly, reaching its maximum value on August 26; there may possibly have been more on August 25 when no determination was made. The curves in Fig. 57

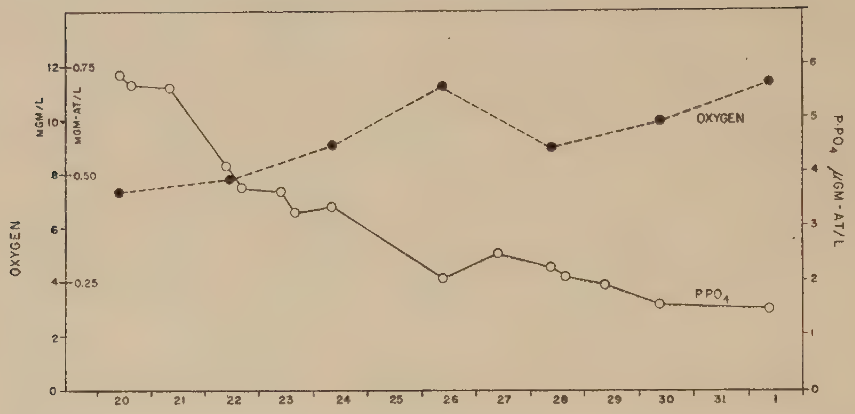

Figure 59. Concentration of phosphate-phosphorus and oxygen in the water of the tank during Experiment 1.

give the impression that the plankton was growing more rapidly than it was making chlorophyll. The second increase in plankton was not matched by chlorophyll.

The data on rate of photosynthesis are of greater interest, since they should be a measure of the rate of production of organic matter by the plankton. The immediate effect of the fertilizer is exhibited by the three measurements which were started on the first day (Table I).

TABLE I. RATE OF OXYGEN CHANGES IN THE THREE INITIAL DETERMINATIONS OF EXPERIMENT 1 SHOWING THE EFFECT OF ADDED NUTRIMENT. RATES OF CHANGE OF OXYGEN CONCENTRATION IN LIGHT AND DARK BOTTLES AND TOTAL RATE OF PRODUCTION (LIGHT—DARK) ARE GIVEN IN TWO DIFFERENT UNITS. THE UPPER FIGURES ARE THE RATES AS MILLIGRAM-ATOMS PER LITER PER DAY, THE LOWER FIGURES IN PARENTHESES ARE THE RATES AS MILLIGRAMS PER LITER PER DAY

	Total oxygen production	*Change in light bottle*	*Change in dark bottle*
Raw sea water (control)	0.030	0.014	−0.016
	(0.48)	(0.22)	(−0.26)
Fertilized with NO_3	0.046	0.030	−0.016
	(0.74)	(0.48)	(−0.26)
Fertilized with NO_3 and PO_4	0.067	0.047	−0.020
	(1.07)	(0.75)	(−0.32)

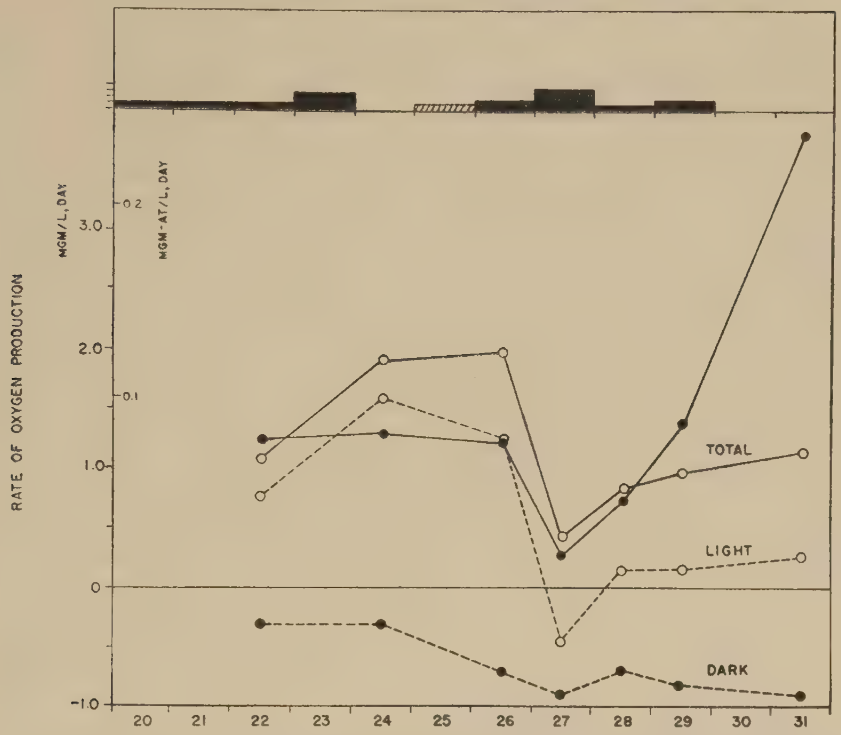

Figure 60. Rates of change of oxygen concentration in light and dark bottles and of total oxygen production (light-dark) in Experiment 1. The rate of oxygen production per milligram of chlorophyll (× 0.01) is shown by the thick solid line and dots. Chlorophyll values used were means of concentrations in tank at beginning and end of the determination. The black band at top represents relative degree of cloudiness in qualitative units shown at left.

Addition of fertilizer had relatively little effect on respiration but increased the rate of production greatly. Addition of nitrate alone made an increase of about 50%, while further addition of phosphate more than doubled the rate in raw sea water. This seems to imply that the population before fertilization had suboptimal quantities of both nutrient substances.

The rate of photosynthesis during the following period varied greatly. The maximum rate of production occurred during the period August 22–28, which includes the date on which the population was increasing the most rapidly and on which chlorophyll concentration was greatest. The minimum rate of production occurred during the period August 26–28, which includes the day during which the

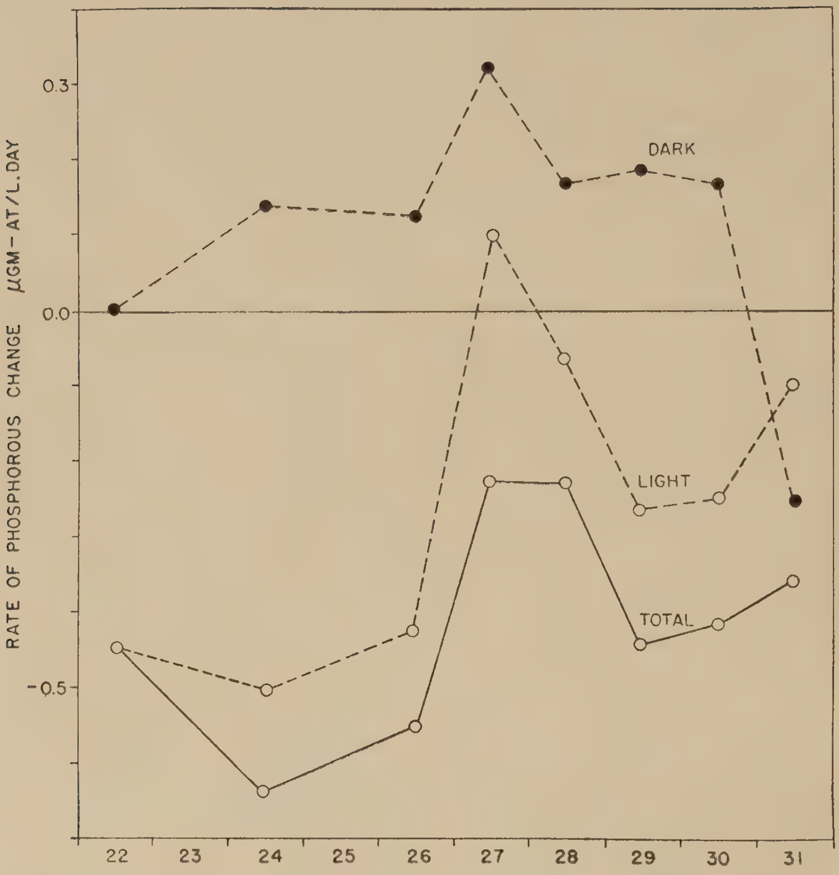

Figure 61. Rate of change of phosphate-phosphorus concentration in light and dark bottles and total consumption (light-dark).

population was decreasing most rapidly. These same rates of oxygen production were recalculated on the basis of the amount of chlorophyll by dividing by the mean amount of chlorophyll in the tank plankton during the period the bottles were exposed. The results, demonstrated by a curve in Fig. 60, show that during the first half of the experiment the rate of production per milligram of chlorophyll was rather uniform. It was very low during the period August 26–28, subsequently increased to a level slightly above the original values, and was very high during August 30–September 1. These large fluctuations are evidently due to variation in the amount of sunlight.

Unfortunately there are no actual measurements of light, but qualitative estimates of the degree of cloudiness were obtained.[5] These estimates are symbolized by the black band at the top of Fig. 60, where thicker bands correspond to more clouds and less light. Cloud and heavy rain during August 27, with moderate clouds before and after, are no doubt responsible for the very low rate of production during August 26–28, while very bright sunshine during August 30–September 1 greatly increased the rate of production per milligram of chlorophyll, although the absolute rate, per liter of water, was not so greatly increased, since there was less chlorophyll. The changes of phosphate and oxygen in the tank (Fig. 59) reflect the changes in production.

In the dark bottles the amount of phosphate always increased. In the light bottles the phosphate decreased, evidently being taken up in the processes leading to formation of new organic material. These changes were calculated as rates and handled exactly as were the oxygen data. This procedure involves assumptions not necessary when considering oxygen. Nevertheless, as seen by comparing Fig. 61 with Fig. 60, there is a very close relation between the utilization of phosphorus and the liberation of oxygen. This relationship is very clearly shown in Fig. 62, where the rates of oxygen production are plotted against the corresponding rates of phosphorus uptake. A line, fitted by eye to pass through the origin, shows that one atom of phosphorus was required under these conditions in the processes which resulted in liberation of about 90 molecules of oxygen, and, of course, fixation of that number of carbon dioxide molecules in carbohydrate. The correlation coefficient was not calculated for these few points, but it obviously would be high.

These figures give information about the ratio in which elements were used by the phytoplankton. The ratio of carbon to phosphorus contained in marine plankton may be taken as 106 : 1 by number of atoms as an average. Assuming that two atoms of oxygen are released for every carbon fixed, this ratio is 1.15 times that for the utilization by tank plankton. However, since only the oxygen that appears in the light bottle represents carbon permanently fixed in the plankton, it may be more reasonable to use the rates of increase of oxygen in the light bottle in the comparison. If this is done, it is found that the ratio in marine plankton is about 1.43 that of utilization. This is quite reasonable considering the nature of the compared figures, and the fact that the tank plankton had ample opportunity to restore any

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[5] Kindly furnished by Mr. Norman T. Allen of the Woods Hole Oceanographic Institution.

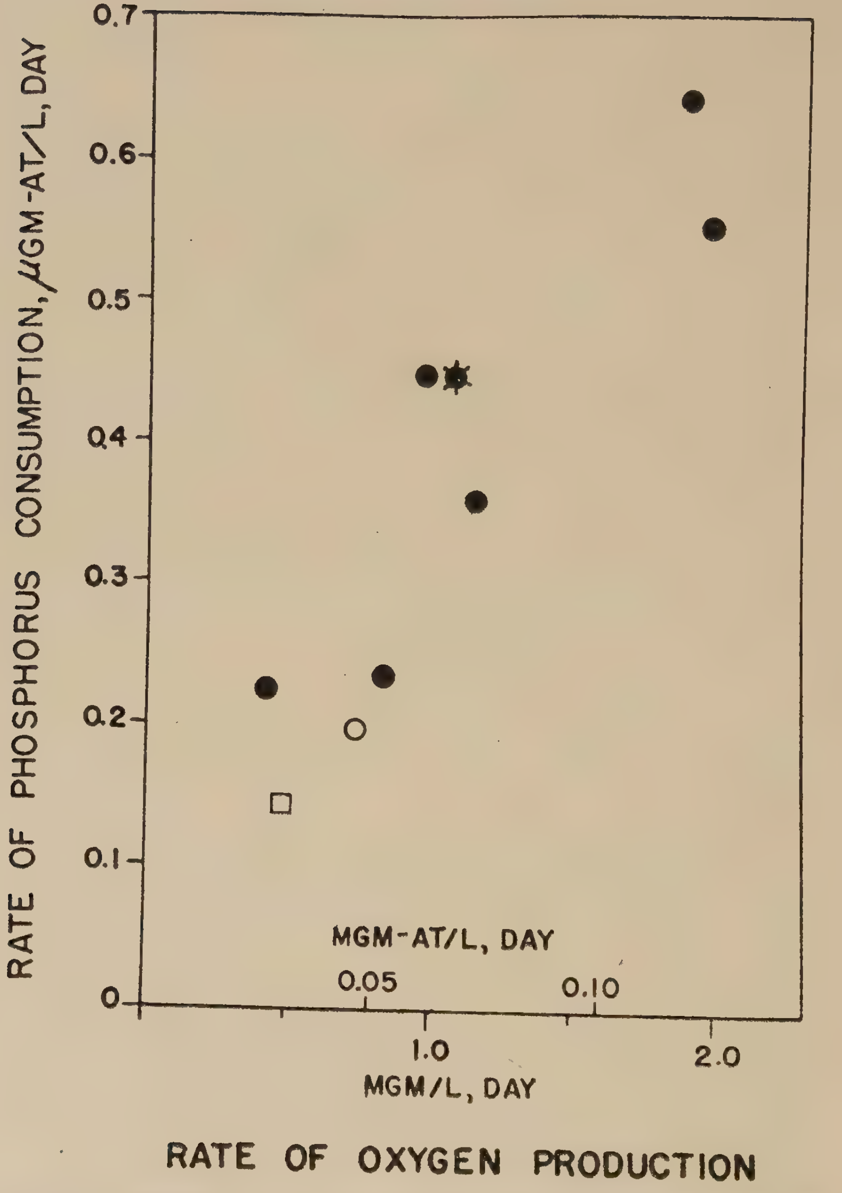

Figure 62. Correlation between total oxygen production and phosphate-phosphorus consumption in Experiment 1. Square symbol represents rates in raw sea water, open circle rates after nitrate fertilization, and starred dot after nitrate and phosphate fertilization. Other points refer to determinations on subsequent days.

phosphorus deficiencies during the initial stages of the experiment. Since data are not available on the utilization of phosphorus within the cells it is not possible to make a more exact calculation.

It was necessary to terminate the work on oxygen production by September 1, although certain observations were continued until November 29, when the tank was emptied. Twice a week temperature and phosphate were measured and plankton counted. The number of cells continued to increase, with large fluctuations, until November 7, when there were 19,000 cells/ml., whereupon the number fell to 1,800 cells/ml. on November 15. The population recovered somewhat by the time of the last collection. Despite the greater number of cells present during September, October and November as compared to August, the volume of phytoplankton remained small, fluctuating irregularly about a level of 0.03 mm^3/ml. This discrepancy is explained by a change in the flora which took place during September, when all the large diatoms and flagellates disappeared, leaving only small species of *Navicula, Nitzschia* and *Prorocentrum.*

This experiment forms the chief basis for the following discussion, but three others should be mentioned as furnishing additional information on the immediate effect of fertilization. The results are given in Table II.

TABLE II. Rate of Oxygen Changes in Experiments 2, 3, and 4, Showing the Effect of Added Nutriment. Rates of Change of Oxygen Concentration in Light and Dark Bottles and Total Rate of Production (Light − Dark) Are Given as Milligram-Atoms per Liter per Day. Further Explanation Is Given in Text

Experiment number	*Location*	*Depth (meters)*	*Before or after fertilization*	*Oxygen Production*		
				Total production	*Change in Light*	*Change in Dark*
2	Tank	0.5	B	0.031	0.013	−0.018
			A	0.161	0.141	−0.020
3	Rand's Harbor	1.5	B	0.026	0.005	−0.021
			A	0.064	0.044	−0.020
4	Rand's Harbor	1.5	B	0.010	−0.001	−0.011
			A	0.031	0.015	−0.016

Experiment 2

The tank was filled on July 10 in the manner previously described, and on July 11 the water was fertilized with an amount of commercial superphosphate calculated to increase the concentration by 5 µg.-at./l.

The highest concentration actually observed was 4.46. By July 15 the concentration of phosphorus was 2.62 µg.-at./l. On this day 92.7 g. of C. P. NH_4NO_3 were added, theoretically increasing the concentration of nitrogen by 154 µg.-at./l. Photosynthesis determinations were started just before and just after nitrate fertilization, and allowed to run four days. During this period the phytoplankton in the tank, mostly *Leptocylindricus*, *Nitzschia* and *Skeletonema* increased from 187 to 3,046 cells/ml.

Experiment 3.

On July 25 the smaller arm of Rand's Harbor was fertilized with commercial nitrate and phosphate fertilizers in amounts calculated (assuming no tidal mixing) to increase the phosphorus by 5 µg.-at/l. and the nitrogen in the same ratio as in Experiment 1. This assumption was not seriously entertained, but it served as a basis for calculation. Just before and after fertilization, bottles for photosynthesis determinations were filled with water from 1.5 m. and suspended at that depth. The initial concentration of phosphorus was 0.87 µg.-at./l. before fertilization, 5.56 afterwards. The initial chlorophyll concentration was 0.011 mg./l.

Experiment 4

Another experiment at Rand's Harbor was started on August 1. The smaller branch was fertilized with commercial superphosphate in an amount calculated to increase the phosphorus concentration by 25.0 mg.-at./l. Because of tidal mixing and distribution, only 4.95 was observed. The initial chlorophyll concentration was 0.010 mg./l. Photosynthesis determinations were made as in Experiment 3, and allowed to run until August 9. This long period was undesirable, but unavoidable, and the figures are probably not very representative of actual production.

DISCUSSION

While the main object of the experiments was to investigate the extent to which fertilization may increase photosynthetic activity, this type of work should also elucidate the relationship between photosynthetic activity and changes in the standing crop of phytoplankton. Obviously, one experiment is not sufficient to furnish data for an extended discussion, particularly as major changes in crop took place over a period of time that was short as compared to the duration of the photosynthesis determinations. It may be pointed out, however, that even under these conditions a fairly consistent relation held during the latter part of the experiment. The change in standing crop was calculated as the mean of the daily relative changes in number during the period covered by each photosynthesis determination. Not figured here, the plotted data may be described as lying quite close to a straight line, except during the first part of the experiment, when the population was presumably rapidly restoring deficiencies, growing, and when phosphorus in the water was still at a high concentration. The significance is difficult to assess with the available data, and it is hoped that this point may be attacked in further work (cf. Riley, 1943).

The pertinence of work of the sort described here to general practices of fertilization needs comment. The authors undertook this work as a study of general problems of productivity in aquatic environments rather than as a study of fertilization. Nevertheless, it is obvious that those who fertilize ponds and saline estuaries to increase fish yields must believe in the reality of nutrient chains, and in order to have a rational basis for fertilization they need information about the effect of fertilization on all steps of production, including the utilization of the added nutrients and the effect on the rate at which organic material is synthesized. It seems improbable that the effect of fertilization in actual fish ponds or natural habitats can be properly judged only by measuring the amount by which the crop of phytoplankton is increased, for the following reasons. If there is a huge increase of long duration in crop after fertilization, the implication is that phytoplankton is not being efficiently consumed, and that therefore inorganic fertilization was not required in the first place, or was insufficient alone. On the other hand, if the phytoplankton crop does not increase much, one is not sure whether the plants for some reason did not respond to the added nutrients, or whether they were kept grazed down by animals. Measurements of photosynthesis in conjunction with measurements of the standing crop would seem to yield information on this point. Measures of the number of intermediate consuming organisms are not sufficient alone to indicate browsing activity, since the mean rate of feeding per animal can vary widely during the year. To be sure, it has been well-demonstrated that it is possible to obtain satisfying yields of fish by fertilizing without studying intermediate steps, but in a scientific investigation of problems of food chains and nutrient cycles, rules of thumb devised empirically for practical purposes are not sufficient.

The determination of chlorophyll seems to the authors to be of critical importance in present day investigations of phytoplankton production. The use of chlorophyll or other plant pigments as a measure of the crop of phytoplankton has been frequently discussed (Riley, 1938; Graham, 1943; Juday, Blair and Wilda, 1943). The basis for this use of such measurements is that chlorophyll is a pigment characteristic of plants, not found in animals except in food or symbiotic algae, and that it is decomposed after the death of the cell. Unfortunately, the amount of chlorophyll per cell evidently can vary, and presumably the process of decomposition is not instantaneous; therefore, chlorophyll may occur to some extent in dead cells or even outside of cells. There appears to be no satisfactory evaluation of the degree to which "dead" chlorophyll can accumulate, nor of the variations in amount per cell. In view of the known sources of error in using cell number, cell volume, and dry weight of material as indices of amount of phytoplankton, one may wonder if chlorophyll may not yet turn out to be useful at least as a supplementary measure of phytoplankton population in that it is subject to less error than some other methods.

Aside from all these considerations the more important significance of chlorophyll is that it is the gate through which practically all energy enters the phytoplankton, and hence the entire biotic association, unless there is fertilization with organic matter. Without chlorophyll, no amount of inorganic fertilizer would accomplish anything. It is therefore a measure of the synthetic potential of a plankton population. However, chlorophyll has certain limitations even as an index of photosynthetic potential, at least in comparing different localities. Attention has been directed at this point by Manning and his collaborators (Manning, Juday and Wolf, 1938; Manning and Juday, 1941), who discuss a number of aspects of the problem. The work of the Wisconsin group has been further summarized by Juday, Blair and Wilda (1943). These authors point out that the rate of photosynthesis is a rather complicated function of light intensity, varying with different species of algae and the density of population. Further, differential absorption of colors by water adds complications. Nevertheless, a better index has not yet been discovered. The expression of rate of photosynthesis per unit of chlorophyll as in Fig. 60 should permit an evaluation of the effect of light intensity upon whatever particular phytoplankton assemblage is under study, with the existing conditions of nutrition. In the papers cited above there is little mention of the nutritive conditions under which the experiments were conducted, and it is not known if the rates of production were inhibited by lack of nutrients; judging by general knowledge of nutritional conditions in nature, it may be supposed that the rates were not as high as possible under the given light and chlorophyll conditions.

It is to be expected that accumulation of information on the matters discussed here will help clarify our understanding of the effectiveness of various types of fertilizations. It may even become possible to make diagnostic experiments with natural phytoplankton populations to determine fertilization programs in practical work.

SUMMARY

1. The immediate effect of fertilization with phosphate or nitrate and phosphate on marine phytoplankton was studied by determining the rate of photosynthesis of the plankton before and after the addition of fertilizer. Two experiments were made in a large concrete tank and two in a salt water bay. The rate of oxygen production was increased by factors of about 1.5 to 5, although respiration was usually affected much less.

2. One of the tank experiments was maintained for a period of thirteen days, during which determinations of photosynthesis and concentration of chlorophyll were made every second day. Daily determinations of phosphate, temperature and phytoplankton concentration were made. During the initial period of rapid growth, the population increased more rapidly than did its chlorophyll. Rate of photosynthesis and growth of the plankton varied with changes in sunlight falling on the tank.

3. There was a close correlation between rate of utilization of phosphate and production of oxygen, and the ratio of the two is close to that expected on the basis of the average chemical composition of plankton organisms.

4. The use of a photoelectric colorimeter in determining chlorophyll is discussed and data presented on the transmission spectrum of the light filters.

5. The application of such studies is discussed.

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Hydrodynamic Properties of Sea Water at the Front of a Shock Wave*†

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The Rankine-Hugoniot relations have been applied to appropriate equation-of-state data in order to calculate the propagation velocity, particle velocity, enthalpy increment, Riemann function, etc. at shock fronts of various amplitudes in sea water. One set of tables provides values over a wide pressure range (up to about 80 kilobars) and is principally intended for use in conjunction with theories of propagation of shock waves originated by underwater explosions. A second set of tables contains values which are closely spaced up to pressures of 14 kilobars. These are calculated with somewhat greater precision and are intended for use in connection with experimental measurements of particle and propagation velocities, etc.

I. INTRODUCTION

It has long been recognized that the velocity of propagation of sound waves of finite amplitude in a fluid medium is a function of the pressure in the wave. Lamb[1] ascribes the early development of the theory to independent investigations of Earnshaw and Riemann. Qualitatively this work indicated that, since the higher pressure portions of a wave travel with greater velocity, an arbitrarily-shaped pressure pulse of finite amplitude must, during propagation, alter its shape in such a manner as to build up into a shock front. By applying the laws of conservation of mass, energy, and momentum to the transfer of matter across the shock front, Rankine and Hugoniot obtained a set of three relations among the five variables: pressure, density, particle velocity (u), shock front

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[1] H. Lamb, *Hydrodynamics* (Cambridge University Press, London, 1932) 6th Ed., p. 481.

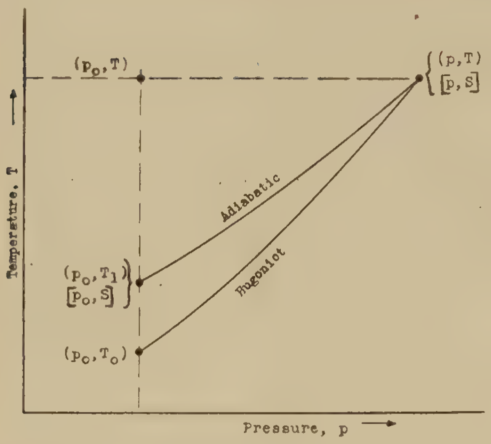

FIG. 1. Adiabatic and Hugoniot contours in $p-T$ plane.

velocity (U), and enthalpy increment (ΔH). These relations, when applied to data on the equation-of-state and specific heat, make it possible to calculate u, U, and ΔH and to evaluate certain other functions applicable to the theory of the formation and propagation of shock waves originated by explosions.[2]

Precise knowledge of u and U also makes it possible to calculate shock wave pressures in cases where the particle velocity or propagation velocity can be measured. The purpose of the calculations described below was to apply the Hugoniot relations to appropriate equation-of-state data for sea water in order to provide (a) tables of the desired functions up to very high pressures (*ca.* 80 kilobars) for use in the theory of propagation of underwater explosion waves,[2] and (b) tables of particle and propagation velocity at fairly close pressure intervals in a lower pressure region (up to *ca.* 14 kilobars).

II. OUTLINE OF THE THEORY AND COMPUTATIONAL PROCEDURES

In this section we give an account of the hydrodynamical and thermodynamical relations, and the computational procedures leading to the numerical results tabulated in Sections III and IV. For the convenience of the reader a glossary of symbols is presented in Appendix III.

When a shock wave advances with velocity U into a stationary fluid of unperturbed pressure p_0 and specific volume v_0, the pressure p, specific volume v, and particle velocity u of the fluid behind the shock front are determined by the Rankine[3]-Hugoniot[4] conditions, which express the conservation of mass, momentum, and energy of an element of fluid passing through the front. For the purposes of this paper, these conditions may conveniently be written

$$u=[(p-p_0)(v_0-v)]^{\frac{1}{2}}, \tag{2.1}$$

$$U=v_0[(p-p_0)/(v_0-v)]^{\frac{1}{2}}, \tag{2.2}$$

$$\Delta H=(1/2)(p-p_0)(v+v_0). \tag{2.3}$$

In the last equation, ΔH is the specific enthalpy increment of an element of fluid when it passes through the front. The specific enthalpy is defined as the sum of the internal energy per gram and the pressure-volume product, pv.

Given equation of state and specific heat data for the fluid, any three of the variables p, v, U and u may be determined as functions of the fourth. Here we shall regard p as the independent variable. For certain hydrodynamic applications we must have, in addition to v, U, and u as functions of p, the sound velocity

$$c=(\partial p/\partial \rho)^{\frac{1}{2}}{}_S; \quad \rho=1/v, \tag{2.4}$$

the Riemann σ-function†

$$\sigma=\int_{p_0}^{p}[v[p',S]/c[p',S]]dp', \tag{2.5}$$

and the undissipated enthalpy

$$\omega=\int_{p_0}^{p}v[p',S]dp', \tag{2.6}$$

where S is the entropy.

In practice, one must resort to successive approximations to effect a reduction of the Hugoniot conditions, combined with equation-of-state and specific heat data, to a set of relations expressing u, U, and v as functions of p. To this

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[2] J. G. Kirkwood and H. Bethe, *The Pressure Wave Produced by an Underwater Explosion* (Dept. of Commerce Bibliography No. PB 32182), OSRD Report No. 588, Part I.

[3] W. J. M. Rankine, Trans. Roy. Soc. London, **A160**, 277 (1870).

[4] H. Hugoniot, J. de l'ecole polyt. **51**, 3 (1887); **58**, 1 (1888).

† The Riemann σ-function occurs in Riemann's form of the hydrodynamical equations, which, for the case of spherical symmetry, may be written (see reference 1):

$$[(\partial/\partial t)+(c+u)(\partial/\partial r)](\sigma+u)=-2cu/r,$$
$$[(\partial/\partial t)-(c-u)(\partial/\partial r)](\sigma-u)=0,$$

where t is the time and r is the radial coordinate. The other quantities have already been defined.

end, it is expedient first to consider certain quantities as functions of pressure and temperature, p and T, or pressure and entropy, p and S. Before proceeding to a more detailed discussion of the calculations it may perhaps help to orient the reader if we consider, qualitatively, contours of some pertinent quantities in the p–T plane. In Fig. 1, the possible states of a given fluid just behind the shock front lie along a single curve, which we have labeled "Hugoniot." An element of fluid initially in the state (p_0, T_0) which has attained a state (p, T) just behind the shock front finally returns to a state (p_0, T_1) along the adiabatic, so labeled in the figure. Also included are the designations of a few points on a p–S basis using square brackets according to the convention introduced in Part b of this section. In general, T_1 is larger than T_0 because of the dissipation occuring at the front. The central part of our problem is the determination of the Hugoniot curve.

We shall consider in Part a the calculations due to Arons and Halverson[5] which are intended to be accurate in the range of relatively low pressure (*ca.* 0 to 20 kilobars). These results as stated in the introduction are intended for the determination of the peak pressure of a shock wave from measured values of the shock front velocity U or particle velocity u. In Part b, we shall consider the calculations of Kirkwood and Richardson,[6] the results of which were originally intended for the applications of the shock wave propagation theory of Kirkwood and Bethe[2] which required data over a higher range of pressures (*ca.* 20 to 50 kilobars).

a. Calculations of Arons and Halverson

Here we outline the calculations[7] suitable for the relatively low pressure range (*ca.* 0 to 20 kilobars) based upon the equation-of-state and specific heat data discussed in detail in Appendix I. For the range 0 to 1.5 kilobars, the Ekman equation-of-state was used; in the range 0 to 25 kilobars, the Tait equation-of-state,

$$v(0, T)-v(p, T)/v(0, T)=(1/n)\log[1+p/B(t)],$$
$$t=(T-273.16)^\circ\mathrm{C}. \quad (2.7)$$

In the first case, the initial temperature was $t_0=15°\mathrm{C}$; in the second, $t_0=25°\mathrm{C}$. In both cases, the initial pressure $p_0=0$. Neither of the two equations-of-state are complete in the sense that $v_0=v(0, T)$ must be determined by auxiliary thermal expansion data (also discussed in Appendix I).

We express the enthalpy and volume increments

$$\begin{aligned}\Delta H&=H(p, T)-H(0, T_0),\\ \Delta v&=v(p, T)-v(0, T_0),\end{aligned} \quad (2.8)$$

in terms of line integrals, first along an isobar from $(0, T_0)$ to $(0, T)$ and, secondly, along an isotherm from $(0, T)$ to (p, T) (see Fig. 1). For the enthalpy increment we obtain

$$\begin{aligned}&\Delta H=\Delta_p H+\Delta_T H,\\ &\Delta_p H=\int_{T_0}^{T} C_p(0, T')dT'=\bar{c}_p\Delta T,\\ &\Delta_T H=\int_0^p\left[v(p', T)-T\frac{\partial v(p', T)}{\partial T}\right]dp',\\ &\Delta T=T-T_0,\end{aligned} \quad (2.9)$$

where $c_p(0, T)$ is the specific heat extrapolated to zero pressure and $\bar{c}_p$ is the mean of c_p over the temperature range ΔT.

For the volume increment we obtain

$$\begin{aligned}&\Delta v=\Delta_p v+\Delta_T v,\\ &\Delta_p v=v(0, T)-v(0, T_0)=\bar{\beta}_0\Delta T,\\ &\Delta_T v=v(p, T)-v(0, T),\end{aligned} \quad (2.10)$$

where $\bar{\beta}_0$ is the mean thermal expansion at zero pressure over the temperature range ΔT.

From the last Hugoniot condition, Eq. (2.3), and Eq. (2.9) we obtain

$$\Delta T=\frac{[v(0, T_0)+(1/2)(\Delta_T v)]p-\Delta_T H}{\bar{c}_p-(1/2)(\bar{\beta}_0 p)}, \quad (2.11)$$

where $\Delta_T H$ is to be calculated by means of the third of Eq. (2.9) and the appropriate equation-of-state, and where $\Delta_T v$ is to be obtained from compressibility data. The right-hand side of Eq. (2.11) depends, of course, on the temperature T. The determination of ΔT is accomplished by the method of successive approximations. A trial

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[5] A. B. Arons and R. R. Halverson, *Hugoniot Calculations for Sea Water at the Shock Front*, OSRD Report No. 6577, NDRC No. A-469.

[6] J. G. Kirkwood and J. M. Richardson, *The Pressure Wave Produced by an Underwater Explosion, Part III*, OSRD Report No. 813 (Dept. of Commerce Bibliography No. PB 32184).

[7] J. G. Kirkwood and E. Montroll, *Pressure Wave Produced by an Underwater Explosion, II*, OSRD Report No. 676 (Dept. of Commerce Bibliography PB-32183).

TABLE I. $U-c_0/c_0$, u, and ΔH in low pressure region (based on Ekman equation-of-state). Sea water: Initial temperature 15°C; salinity 32 parts per thousand (3.79 wt. percent NaCl); $c_0=4922.8$ ft/sec $=1500.5$ m/sec.

A				*B*			
$p-p_0$ (kbar)	$\frac{U-c_0}{c_0}$ (%)	u (m/sec)	ΔH (cal/gm)	$p-p_0$ (lb/in²)	$\frac{U-c_0}{c_0}$ (%)	u (ft/sec)	ΔH (cal/gm)
0.00	0.00	0.0	0.0	0	0.00	0.0	0.0
.25	2.07	15.1	5.8	2,000	1.14	29.1	3.2
.50	4.03	31.2	11.5	4,000	2.27	57.6	6.4
.75	5.93	46.2	17.2	6,000	3.35	85.5	9.6
1.00	7.81	60.5	23.0	8,000	4.43	112.9	12.7
1.25	9.65	74.4	28.5	10,000	5.48	139.7	15.9
1.50	11.44	87.7	34.1	12,000	6.53	166.0	19.0
				14,000	7.56	191.8	22.1
				16,000	8.58	217.1	25.2
				18,000	9.59	242.0	28.3
				20,000	10.57	266.5	31.4
				22,000	11.55	290.6	34.5

TABLE II. $U-c_0/c_0$, u, and ΔH in intermediate pressure region (1.5 to 25 kilobars) (based on Tait equation-of-state; $n=7.800$, $B=3.012$). Sea water: Initial temperature 25°C; salinity 32 parts per thousand (3.79 wt. percent NaCl): $c_0=5014.7$ ft/sec $=1528.5$ m/sec.

A				*B*			
$p-p_0$ (kbar)	$\frac{U-c_0}{c_0}$ (%)	u (m/sec)	ΔH (cal/gm)	$p-p_0$ (lb/in²)	$\frac{U-c_0}{c_0}$ (%)	u (ft/sec)	ΔH (cal/gm)
0.0	0.00	0.0	0.0	0	0.0	0	0.0
1.0	8.18	59.2	23.0	20,000	11.0	258	31.3
1.5	11.88	85.5	34.2	30,000	15.8	375	46.6
2.0	15.39	110.1	45.3	40,000	20.5	483	62.0
2.5	18.71	135.0	56.3	50,000	24.7	584	77.0
3.0	21.88	157.8	67.2	60,000	28.7	676	92.0
4.0	27.84	200.5	88.8	70,000	32.5	767	107.0
5.0	33.39	240.2	110.1	80,000	36.0	853	121.0
6.0	38.59	277.5	131.2	90,000	39.4	937	135.0
8.0	48.13	346.1	172.9	100,000	42.8	1014	150.0
10.0	56.73	408.9	214.0	120,000	49.2	1168	178.0
12.0	64.70	466.9	254.8	140,000	55.2	1312	207.0
14.0	72.25	510.9	295.2	160,000	60.8	1445	235.0
25.0	108.40	769.1	514.4	180,000	66.3	1564	263.0
				200,000	71.5	1662	291.0

value of ΔT is used in evaluating the right-hand side giving a more accurate value of ΔT on the left-hand side, and the process is repeated until the results of two successive steps differ by a sufficiently small amount. One or two steps generally suffice.

We have thus obtained T as a function of p along the Hugoniot curve (see Fig. 1). It is now possible to calculate immediately the particle velocity u, the propagation velocity U, and the specific volume v as functions of p behind the shock front. The results using the Ekman equation-of-state and the Tait equation-of-state are tabulated in Tables I and II, respectively, of Section III.

b. The Calculations of Richardson and Kirkwood

Here we outline the calculations[6] intended for the applications of the shock wave propagation theory of Kirkwood and Bethe.[2] These are based upon the equation-of-state and specific heat data discussed in detail in Appendix II. We use a modified Tait equation-of-state connecting $v(p, T)$ and $v(0, T)$ to be discussed below. In most respects, the data is made to fit the properties of an aqueous 0.7 molal NaCl solution assumed to be roughly equivalent to sea water of salinity $s=32$ parts per thousand (see Section 1 of Appendix I).

In these calculations the initial pressure p_0 is taken to be zero, and several different initial temperatures T_0 are used: 0°C, 20°C, and 40°C.

Before indicating the precise nature of the modification of the Tait equation, it is desirable to mention that in this part two different pairs of independent variables will be used: pressure and temperature (p, T), and pressure and entropy $[p, S]$. Consequently, in order to indicate which pair are used in a function, we will use parenthesis to indicate the first pair and square brackets to indicate the second, i.e. $v(p, T)$ and $v[p, S]$.

The modified form of Tait equation introduced by Kirkwood[2, 6] is

$$\log(v_1/v)=(1/n)\log(1+p/A[S]), \quad (2.12)$$

where

$$v=v[p, S]=v(p, T[p, S]), \quad v_1=v[0, S],$$

(see Fig. 1) n is an empirical constant, and the function $A[S]$ is related to the function $B(t)$ in the original isothermal form of the Tait equation, Eq. (2.7), as follows,

$$A[S]=B(t[0, S]), \quad t=(T-273.16)°\text{C}. \quad (2.13)$$

The reasons for introducing this modification of the Tait equation are at least twofold: (1) the anomaly of a vanishing specific volume $v(p, T)$ at a finite pressure along a given adiabatic (which does not differ markedly from the Hugoniot curve in the case of water) is removed to a higher pressure by replacing $[v(0, T)-v(p, T)]/[v(0, T)]$

TABLE III. Values of $U-c_0/c_0$ for different temperatures and salinities at a shock wave peak pressure of 1.00 kilobar.

Salinity (parts per 1000)	Temperature (°C)	$U-c_0/c_0$ (%)
32	15	7.81
32	25	7.81
35	15	7.76

by $\log(v[0, S]/v[p, S])$, and (2) the calculation of quantities defined by line integrals along adiabatics is greatly simplified by taking S instead of T as one of the independent variables.

The function $A[S]$ is related simply to c_1, the sound velocity at zero pressure and entropy S according to Eq. (2.4) as follows

$$A[S]=c_1^2/nv_1; \quad c_1=c[0, S]. \tag{2.14}$$

On the basis of Bridgman's p–v–T data for pure water, an average value of n equal to 7.15 has been selected for the present calculations. In Section 2 of Appendix II, it is shown that n deviates from this value by less than 4 percent in a large pressure-temperature field bounded by adiabatics starting at zero pressure and temperatures of 20°C and 60°C, respectively, and extending to pressures of 25,000 kg/cm². We assume that n has the same value for an aqueous 0.7 molal NaCl solution as for pure water, and we obtain by interpolation the required values of $B(t)$ from R. E. Gibson's values of $B(t)$ for dilute aqueous NaCl solutions (see Appendix II, Section 1). The appropriate heat capacity and thermal expansion data are discussed in Section 1 of Appendix II.

We now proceed to the calculation of the quantities u, U, c, σ, and ω. We first express these quantities with use of Eq. (2.12) in terms of p,

$$v=v(p, T)=v[p, S], \quad v_0=v(0, T_0),$$

$v_1=v(0, T_1)=v[0, S]$, and $c_1=c(0, T_1)=c[0, S]$ (see Eqs. (2.1)–(2.6), also Fig. 1) as follows:

$$u=[p(v_0-v)]^{\frac{1}{2}}, \tag{2.15}$$

$$U=pv_0/u, \tag{2.16}$$

$$c=c_1(v_1/v)^{(n-1)/2}, \tag{2.17}$$

$$\sigma=\frac{2c_1}{n-1}[(v_1/v)^{(n-1)/2}-1], \tag{2.18}$$

$$\omega=\frac{c_1^2}{n-1}[(v_1/v)^{n-1}-1], \tag{2.19}$$

Once the temperature T_1, to which an element of fluid returns along the adiabatic intersecting the Hugoniot curve at (p, T), is determined, all of the above quantities may be determined as functions of p. To accomplish this, the enthalpy increment, ΔH, occurring in the third Hugoniot condition, Eq. (2.3), is written as the sum of two line integrals, the first along an isobar from $(0, T_0)=[0, S_0]$ to $(0, T_1)=[0, S]$ and the second along an adiabatic from $(0, T_1)=[0, S]$ to $(p, T)=[p, S]$ (see Fig. 1), giving:

$$\Delta H=\omega+h,$$

$$\omega=\int_0^p v[p', S]dp', \tag{2.20}$$

$$h=\int_{S_0}^{S} T[0, S']dS'=\int_{T_0}^{T_1} c_p(0, T')dT',$$

where ω is the undissipated enthalpy already defined by Eq. (2.6) with $p_0=0$ and given explicitly in terms of c_1, v_1, and v in Eq. (2.19). The dissipated enthalpy h can be determined as an explicit function of T_0 and T_1 from specific heat data (Appendix II, Section 1). Combining the third Hugoniot condition, Eq. (2.3), with Eqs. (2.19) and (2.20) we obtain the relation

$$\frac{h}{c_1^2}=\frac{1}{2n}\left[y-\frac{n+1}{n-1}(y^{(1-1/n)}-1)-y^{-1/n}\right]-\frac{v_1-v_0}{2nv_1}(y-1), \tag{2.21}$$

TABLE IV. Properties of sea water at a shock front. (Initial temperature 0°C; salinity 0.7 m NaCl; $C_0=1443$ m/sec.)

p (kilo-bar)	u (m/sec)	U (m/sec)	c (m/sec)	σ (m/sec)	$\omega\times10^{-6}$ (m/sec)²	h (joule/gm)	v (cm³/gm)
0	0	—	—	0	0	0	0.9915
5	257.0	1930	2190	253.5	0.4565	6.740	.8593
10	433.0	2290	2720	420.5	0.8720	25.80	.8040
15	575.0	2585	3145	552.0	1.270	54.40	.7710
20	697.5	2845	3510	664.0	1.655	86.55	.7483
25	805.5	3075	3835	763.5	2.030	122.5	.7319
30	905.0	3285	4125	855.5	2.405	160.5	.7186
35	997.0	3480	4395	940.5	2.770	201.5	.7075
40	1080	3665	4640	1020	3.140	244.0	.6989
50	1240	4000	5095	1175	3.860	331.0	.6842
60	1385	4300	5495	1315	4.575	419.0	.6728
70	1515	4585	5870	1455	5.285	509.0	.6641
80	1635	4855	6225	1585	6.000	595.5	.6579
90	1740	5120	6570	1705	6.730	676.0	.6542

TABLE V. Properties of sea water at a shock front. (Initial temperature 20°C; salinity 0.7 m NaCl; $C_0=1517$ m/sec.)

p (kilo-bar)	u (m/sec)	U (m/sec)	c (m/sec)	σ (m/sec)	$\omega\times10^{-6}$ (m/sec)²	h (joule/gm)	v (cm³/gm)
0	0	—	—	0	0	0	0.9929
5	251.0	1975	2230	248.5	0.4595	5.570	.8668
10	425.5	2335	2755	415.5	0.8790	23.45	.8120
15	567.0	2630	3175	549.0	1.280	49.35	.7787
20	689.0	2880	3535	663.0	1.670	80.05	.7555
25	798.0	3110	3855	765.0	2.050	115.0	.7381
30	897.5	3320	4140	859.0	2.425	152.5	.7243
35	990.0	3510	4405	946.5	2.795	192.0	.7130
40	1075	3690	4650	1030	3.160	233.0	.7034
50	1235	4020	5100	1185	3.885	317.5	.6880
60	1380	4325	5505	1330	4.605	404.5	.6765
70	1510	4610	5880	1465	5.320	489.5	.6679
80	1625	4885	6240	1600	6.050	573.5	.6626

TABLE VI. Properties of sea water at a shock front. (Initial temperature 40°C; salinity 0.7 m NaCl.)

p (kilo-bar)	u (m/sec)	U (m/sec)	c (m/sec)	σ (m/sec)	$\omega \times 10^{-6}$ (m/sec)^2	h (joule/gm)	v (cm^3/gm)
0	0	—	—	0	0	0	0.9993
5	249.5	2005	2255	247.0	0.4630	5.59	.8749
10	423.5	2360	2775	415.0	0.8870	22.75	.8198
51	566.5	2645	3195	550.0	1.290	48.30	.7859
20	689.0	2900	3550	666.5	1.685	78.70	.7621
25	798.5	3130	3865	770.5	2.065	113.5	.7441
30	899.0	3335	4150	866.0	2.445	151.0	.7298
35	992.0	3525	4415	955.5	2.815	189.5	.7179
40	1080	3705	4660	1040	3.185	230.5	.7080
50	1240	4035	5110	1200	3.915	315.0	.6926
60	1380	4340	5515	1345	4.640	400.5	.6813
70	1510	4635	5900	1485	5.370	483.0	.6737

where $y=(v_1/v)^n$. With the aid of tables of n/c_1^2 and v_1 as functions of T_1 and T_0, Eq. (2.21) may be solved by successive approximations giving T_1 as a function of the parameter y. Since the equation of state, Eq. (2.12), may be expressed simply as $p=B(T_1-273.16)[y-1]$, the temperature T_1 may be determined as a function of the pressure p by a tabular elimination of y. By graphical interpolation, T_1 is finally determined for the desired integral values of p (in kilobars), and the functions u, U, c, σ, and ω are then computed as functions of p by means of Eqs. (2.15)–(2.19).

III. NUMERICAL RESULTS OF ARONS AND HALVERSON

In fundamental shock wave studies, it is frequently necessary to know values of $U-c_0/c_0$ and u at given pressure levels to the highest possible degree of accuracy. With this object in view, the calculation methods described in Section 2A were applied to the best available equation-to-state data. The numerical results are given in Tables I and II. A critical discussion of the equation-of-state data will be found in Appendix I together with references to the sources from which they were obtained.

Table I gives results for the "low pressure" region, covering shock wave peak pressures of from 0 to 1.50 kilobars (*ca.* 22,000 p.s.i.). The calculations in this table were based upon the Ekman equation-of-state for sea water (see Appendix I) which is used in the calculation of sound velocity for echo-ranging tables.

Since the Ekman equation deviates appreciably from experimental compressibility data at pressures exceeding 2 kilobars, this equation was abandoned in the "intermediate pressure" region. The results in Table II are applicable principally to the region between 1.5 and 14 kilobars (*ca.* 200,000 p.s.i.) and are based on a careful fit of the Tait equation to Adams's experimental compressibility data (see Appendix I).

Tables I and II were computed for certain specific values of temperature and sea water salinity (equivalent to 0.675 molal NaCl), and it is shown in Table III that the value of $U-c_0/c_0$ is not very sensitive to changes in these variables.

IV. NUMERICAL RESULTS OF KIRKWOOD AND RICHARDSON

In Tables IV to VI, the particle velocity u, the shock front velocity U, the sound velocity c, the Riemann σ-function, the undissipated enthalpy ω, the dissipated enthalpy h, and the specific volume v of sea water (0.7 molal NaCl solution) are presented as functions of pressure p along three Hugoniot curves, starting at zero pressure and the temperatures 0°C, 20°C and 40°C, respectively. These results have been calculated by the procedures of Part b of Section 2 and the data of Appendix II. The results above 30 kilobars represent extrapolations beyond the range of experimental data; consequently the validity of the results above, say, 50 kilobars, is questionable.

In closing this discussion of the calculations, the authors wish to acknowledge their gratitude and appreciation to Professor J. G. Kirkwood of Cornell University for his contributions in initiating the work and in supplying valuable guidance and advice.

APPENDIX I††

1. Salinity and Temperature Conditions

All calculations were made for sea water having a salinity of 32 parts per thousand (the average salinity of sea water at Woods Hole, Massachusetts). Salinity is defined in terms of directly measured chlorinity as:

$$s=0.030+1.8050\ \mathrm{Cl}$$

where s and Cl are expressed in parts per thousand.

It was calculated from the average composition

[††] Equation-of-state data used in computation of Tables I and II.

of sea water that (on the basis of *ionic strength*) a salinity of 32 parts per thousand is equivalent to an NaCl solution having a molality of 0.675 or a weight percentage of 3.79 percent NaCl.

Table I was computed for an initial temperature of 15°C because this temperature is a rough average of conditions normally encountered in experimental work. Table II was computed for an initial temperature of 25°C because this was the temperature quoted for the available compressibility data.[8] Table III shows that the results are not sensitive to small variations in temperature and salinity.

2. Specific Volume and Coefficient and Thermal Expansion

The best sources of data seem to be the oceanographical tables of Knudsen.[9] Second power equations in t(°C) were fitted to the data tabulated for $s=32$:

For Table I:

$$v(t)=0.97709+2.05\times10^{-4}(t-15)+4\times10^{-6}(t-15)^2.$$

For Table II:

$$v(t)=0.97956+2.85\times10^{-4}(t-25)+4\times10^{-6}(t-25)^2.$$

3. Heat Capacity

The heat capacity data used in computing Tables I and II are those quoted by S. Kuwahara:[10]

$$C_p=C_{p'}-0.0004226t+0.000006321t^2\text{ cal./gm°C},$$

where

$$C_{p'}=1.005-0.004136s+0.0001098s^2-0.000001324s^3.$$

In the above equations, t is temperature in °C and s is salinity in parts per 1000. These data are in good agreement with those used by Kirkwood and Richardson, quote in Appendix II.

TABLE VII. Comparison of experimentally measured sound velocity with calculations based on the Ekman Compressibility Equation. (Salinity=31.7 parts per thousand.)

Temperature (°C)	Velocity of sound (ft/sec) Measured	Calculated	Deviation (%)
10.9	4887.7	4875.6	0.26
11.6	4885.8	4883.8	0.04
11.6	4893.1	4883.8	0.19
11.5	4902.4	4882.5	0.41
11.1	4888.3	4878.5	0.20

TABLE VIII. Comparison of Adams's experimental compressibilities and the empirical fit given by the Ekman and Tait equations.

	$(v_0-v)/v_0$				
	Adams (experimental)		Ekman equation	Tait* equation	
P (kbar)	Pure H_2O	3.79% NaCl	$S=32$ (Table I)	$n=7.800$ $B=3.012$ (Table II)	$n=7.445$ $B=3.156$
0.0	0.0000	0.0000	0.0000	0.0000	0.0000
0.5	.0212	.0196	.0198	.0197	.0198
1.0	.0393	.0368	.0370	.0368	.0370
1.5	.0555	.0522	.0522	.0518	.0522
2.0	.0699	.0658	.0655	.0653	.0659
3.0	.0945	.0894	.0871	.0887	.0897
4.0	.1152	.1091	—	.1083	.1095
5.0	.1330	.1265	—	.1254	.1275
6.0	.1485	.1417	—	.1405	.1431
7.0	.1622	.1552	—	.1540	.1569
8.0	.1746	.1670	—	.1662	.1695
9.0	.1858	.1781	—	.1775	.1812
10.0	.1964	.1886	—	.1876	.1917
11.0	.2059	.1980	—	.1972	.2017

* $(v_0-v)/v_0=(1/n)\log(1+p/B)$.

4. Compressibility Data for Low Pressure Region (Table I)

The following equation was used in computing Table I:

$$10^5\mu=\frac{4886}{1+0.183p}-[227+28.33t-0.551t^2+0.004t^3]+p[105.5+9.50t-0.158t^2]-1.5p^2t-\left(\frac{\gamma-28}{10}\right)[147.3-2.72t+0.04t^2-p(32.4-0.87t+0.02t^2)]+\left(\frac{\gamma-28}{10}\right)^2[4.5-0.1t-p(1.8-0.06t)],$$

where p is pressure in kilobars, t is temperature in degrees centigrade, and μ is defined by:

$$v=v_0(1-\mu p),$$

γ is defined by:

$$\gamma=-0.069+1.4708\text{ Cl}-0.001570\text{ Cl}^2+0.0000398\text{ Cl}^3.$$

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[8] Adams, J. Am. Chem. Soc. **53**, 3769 (1931).

[9] *Oceanographical Tables*, Comissariat of Agriculture, USSR, Moscow, 1931. (A general compilation of oceanographic data by N. N. Zubov.)

[10] S. Kuwahara, *Velocity of Sound in Sea Water and Calculation of the Velocity for Use in Sonic Sounding* (Hydrographic Dept. I.J.N. Tokyo, 1938).

The above empirical equation for sea water compressibility is due to Ekman[11] and has been widely used for computation of sound velocity in sea water.[10,12] The validity of the Ekman equation for sound velocity calculations was verified experimentally as indicated in Table VII.

Experimental sound velocity measurements were made by recording with a rotating drum camera the signals applied to a cathode ray oscilloscope by two very small piezoelectric gauges placed a known distance apart. The sound source was a No. 8 detonator cap placed far enough away from the gauges so that the effect of finite pressure amplitude was less than 0.03 percent. An error of about 0.2 percent was inherent in the experimental work owing to slight errors in the alignment of the two recording gauges with the sound source. This accounts for the magnitude and systematic nature of the discrepancy apparent in Table VII.

Further verification of the applicability of Ekman's equation in the region up to 1.50 kilobars is given in Table VIII where values obtained from the equation are compared with the experimental values of Adams for NaCl solutions.

5. Compressibility Data for Intermediate Pressure Region (Table II)

As indicated in Part 1 of this appendix, a sea water salinity of 32 parts per thousand corresponds to a 3.79 weight percent solution of NaCl. The compressibility of NaCl solution of this concentration was obtained by graphical interpolation of Adams's data.[8]

The Tait equation in the form:

$$v(0,\,T)-v(p,\,T)/v(0,\,T)=(1/n)\,\log[1+p/B(t)],\qquad t=(T-273.16)^\circ\mathrm{C}$$

was then fitted to Adams's data. In an effort to check the Tait equation against the Ekman equation used for computation of Table I, a fit was first made to the lower pressure region. Values of n and $B(25^\circ\mathrm{C})$ were so selected that the equation not only fitted the data of Adams with adequate precision but also yielded the correct velocity of sound in the limit of zero pressure. This additional restriction (that the equation give $c_0=1528$ m/sec. at 25°C and $s=32$) required that $nB(25^\circ\mathrm{C})=23.497$, the latter relation being obtained from the thermodynamic equations:

$$\left(\frac{\partial v}{\partial p}\right)_T=-\frac{v_0^2}{c_0^2}-\frac{T}{c_p}\left(\frac{\partial v}{\partial T}\right)_p^2,$$

$$\left(\frac{\partial v}{\partial p}\right)_T=-\frac{v_0}{nB(t)}\quad\text{at } p=0.$$

In this case n was taken as 7.445 and $B(25^\circ\mathrm{C})$ as 3.156 kilobars, and the resulting equation fits the data of Adams quite closely up to pressures of about 4 kilobars as shown in Table VIII. For purposes of further calculation, the temperature *variation* of B was assumed to be the same as that used by Kirkwood and Richardson on the basis of a private communication from Gibson (see Appendix II). Calculation of $U-c_0/c_0$ at 1.00 kilobar yielded a value of 7.85 percent, in good agreement with the value of 7.81 percent obtained from the Ekman equation.

TABLE IX. Values of n computed from $p-v-T$ data (using $n=7.15$ in computation of ΔT).

t* (°C)	p (kg/cm²) 5000	15,000	25,000
20	7.211	7.183	7.130
40	7.360	7.126	6.969
60	7.411	7.054	6.868

* t_0 = centigrade temperature through which the adiabatic for S passes at zero pressure.

Having verified the accuracy of results obtained from the Tait equation when fitted as described above, the same technique was used to fit the equation to the intermediate pressure range (up to values for 11 kilobars quoted by Adams; it was assumed safe to extrapolate the resulting equation to pressures of 14 or 15 kilobars). It was found that the best fit of the data as well as a correct value for the velocity of sound were obtained by taking $n=7.800$ and $B(25^\circ\mathrm{C})=3.012$, the temperature variation of B again being assumed to be that mentioned above. The Tait equation containing these parameters was then used for the computation of Table II. The fit of the equation to Adams's data is shown in Table VIII.

APPENDIX II

1. Data Employed in the Computations of Part B of Section II

In the modified Tait equation, Eq. (2.12), the function $A[S]=B(t)$, where $t=T[0,\,S]-273.16$, is determined from the empirical values of $B(t)$, fitting the original isothermal Tait equation, Eq. (2.7), to experimental data. R. E. Gibson[13] gives third-degree t-expansions of $B(t)$ for various molalities of NaCl. By interpolating the coefficients (the constant term numerically and the other graphically) for a molality of 0.7, one obtains $B(t)=3.134-1.65\times10^{-3}(t-55)-1.181\times10^{-4}(t-55)^2+5.32\times10^{-7}(t-55)^3$ kilobars.

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[11] V. W. Ekman, *Publications de Circonstance No. 43* (Conceil Permanent Internationale Pour L'Exploration de la Mer. November 1908).

[12] Matthews, *Tables of the Velocity of Sound in Pure Water and Sea Water for Use in Echo Sounding and Sound Ranging* (Hydrographic Dept., Admiralty, H.D. No. 282).

The specific heat $c_p(0, T)$ for a 0.7 molal NaCl solution was obtained by interpolation from the values quoted in the *International Critical Tables* and *Physikalischchemische Tabellen*. The resulting set of values is fitted adequately by the expression

$$c_p(0, t+273.16)=3.9644+6.24\times10^{-4}t \text{ joule/gm. deg.}$$

From Gibson and Loeffler[14] a set of values of $v(0, T)$ covering the range from 25°C to 95°C inclusive was obtained for a 0.7 molal NaCl solution by means of empirical equations giving $v(0, T)$ as a function of concentration for each temperature. In extrapolating to higher temperatures, the relation,

$$v(0, t+273.16)=0.994150+2.929\times10^{-4}(t-25)+3.241\times10^{-6}(t-25)^2 \text{ cm}^3\text{/gm.}$$

was used; for lower temperatures ($t<10$°C),

$$v(0, t+273.16)=0.991442+6.025\times10^{-6}(t-3.8)^2 \text{ cm}^3\text{/gm.}$$

2. Test of the Modified Tait Equation with Bridgman's Data for Pure Water. Determination of the Characteristic Constant n.

The modified Tait equation-of-state, Eq. (2.12), may for our present purposes be written in the form

$$\log(v[0, S]/v[p, S])=(1/n)\log(1+p/A[S]) \qquad \text{(II-1)}$$

where $A[S]$ is related to the $B(t)$ in the original isothermal equation of state as follows,

$$A[S]=B(t_0),\quad t_0=T_0-273.16,\quad T_0=T[0, S]. \qquad \text{(II-2)}$$

According to the convention introduced in Part B of Section II, parentheses ( ) after a function denotes that the independent variables are p and T, whereas square brackets [ ] denote that they are p and S.

Now we wish to test Eq. (II-1) with Bridgman's[15] p–v–T data for pure water with the ultimate object of finding the best value for n. We assume implicitly that n does not vary rapidly with NaCl concentration. To make the comparison, we first must know the values of the temperature T corresponding to the various points $[p, S]$, the calculation of which we consider below.

Letting $T(0, S]=T_0$, $T[p, S]=T$, and $T-T_0=\Delta T$, we have

$$\Delta T=\int_0^p \frac{\partial T[p, S]}{\partial p}dp=\int_0^p \frac{\partial v[p, S]}{\partial S}dp. \qquad \text{(II-3)}$$

Using Eq. (II-1), a simple calculation yields

$$\Delta T=\frac{G}{(1+p/A)^{1/n}}[(1+D)(1+p/A)-(n+D)(1+p/A)^{1/n}+n-1], \qquad \text{(II-4)}$$

where

$$A=A[S]=B(t_0),$$

$$G=\frac{A'[S]v[0, S]}{n-1}=\frac{T_0B'(t_0)\cdot v(0, T_0)}{(n-1)\cdot c_p(0, T_0)},$$

$$D=\frac{nA[S]\dfrac{\partial v[0, S]}{\partial S}}{A'[S]v[0, S]}=\frac{nB(t_0)\beta_0}{B'(t_0)v(0, T_0)},$$

$$\beta_0=\left(\frac{\partial v(0, T)}{\partial T}\right)_{T=T_0}.$$

To calculate T, given a specified p and $T_0=T[0, S]$, a tentative value of $n=7.15$ was chosen for use in Eq. (II-4). The corresponding value of $v[p, S]=v(p, T)$ was obtained by interpolation from Bridgman's[15] p–v–T data. Inserting these values of $v[p, S]$ in Eq. (II-1), and knowing the values of $v[0, S]=v(0, T_0)$ and $B(t_0)$ for pure water, a set of values of n was calculated for $p=5{,}000$, $15{,}000$, $25{,}000$ kg/cm^2

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[13] Private communication.

[14] Gibson and Loeffler, J. Am. Chem. Soc. **53**, 443 (1941).

[15] Bridgman, J. Chem. Phys. **3**, 597 (1935) and private communication.

and $t_0 = T_0 - 273.16 = 20°, 40°, 60°C$, the results summarized in Table IX.

Additional data (for pure water) used in Eqs. (II-1) and (II-4) were

$$B(t) = 2.996 + 7.285\times 10^{-3}(t-25) - 1.790 \times 10^{-4}(t-25)^2 + 6.13\times 10^{-7}(t-25)^2 \quad \text{kilobars,}^{13}$$

and

$$\frac{1}{2.303}\frac{\partial \log v(0, 273.16+t)}{\partial t} = \frac{2(t-3.98)}{244{,}860+15{,}040(t-3.98)^{0.62}} - \frac{(0.62)(15{,}040)(t-3.98)^{1.62}}{[244{,}860+15{,}040(t-3.98)^{0.62}]^2}$$

obtained from Ipatov's[16] empirical equation for v by differentiation.

The average value of n is 7.146. In the present calculations this value has been rounded off to 7.15.

The entries in Tables IV, V, and VI therefore contain more significant figures than the test justifies. On the basis of the test, the errors associated with the use of the modified Tait equation are of the order of several percent. In particular, the results obtained for low pressures will disagree with known data by several percent.

APPENDIX III

Symbols

$A[S]$ = parameter in modified ("adiabatic") Tait equation-of-state.
$B(t)$ = parameter in isothermal Tait equation-of-state.
c = local velocity of sound.
c_0 = velocity of sound at zero pressure.
c_p = specific heat at constant pressure.
h = dissipated enthalpy increment: $\int_{T_0}^{T} c_p(0, T')dT'$.
ΔH = enthalpy increment: $\Delta H = \omega + h$.
n = characteristic constant in Tait equation-of-state.
p_0 = initial pressure ahead of shock front, $p_0 = 0$, in these calculations.
p = pressure behind shock front.
S = entropy.
s = sea water salinity.
t = temperature in °C.
T = absolute temperature.
u = particle velocity behind shock front.
U = shock front propagation velocity.
v_0 = specific volume of medium ahead of shock front.
v = specific volume of medium behind shock front.
$\bar{\beta}_0$ = mean compressibility at zero pressure over temperature range ΔT.
ρ = density.
σ = Riemann function: $\int_{p_0}^{p} \frac{v[p', S]}{c[p', S]} dp'$.
ω = undissipated enthalpy increment: $\int_{p_0}^{p} v[p', S]dp'$.

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[16] I. V. Ipatov, J. Phys. Chem. (U.S.S.R.) 5, 1230 (1934).

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Recent Changes in Sedimentation in the Gulf of Mexico

Parker D. Trask, Fred B. Phleger, Jr., and Henry C. Stetson[1]

THAT SEDIMENTS IN THE GULF OF Mexico have changed materially in relatively recent time has been established by a recent expedition of the *Atlantis*, the oceanographic research vessel of the Woods Hole Oceanographic Institution. Deposits clearly associated with the Ice Age lie within a foot or two of the surface of the sea floor over a large part of the Gulf.

The *Atlantis* spent the months of February and March 1947 in the northwest part of the Gulf of Mexico, primarily for the purpose of investigating the environmental conditions of deposition of sediments. The expedition was sponsored jointly by the Woods Hole Oceanographic Institution and the Geological Society of America. The latter contributed a grant of $14,500 for this purpose to the authors of this communication, while the Oceanographic Institution supplied the vessel, crew, and scientific personnel for the expedition and made available laboratory facilities and personnel for working up the results.

Despite considerable rough weather, the expedition was remarkably successful. Some 550 short cores of the bottom sediments, ranging in length from 5 to 50 cm., and 100 long cores, ranging in length from 1.5 to 3.3 m., were collected. Twelve lines of samples transverse to the coast across the continental platform from the mouth of the Rio Grande to the mouth of the Atchafalaya River, and 7 lines across the continental slope out to the deepest part of the Gulf, were taken. In addition, about 100 stations were occupied for plankton tows, serial temperature, and samples of water. Several hundred temperature-depth records were made with a bathythermograph along the lines of traverse, and continuous depth records were made with a recording fathometer. The material collected is now being actively worked up at the Woods Hole Oceanographic Institution. The U. S. Bureau of Mines Experimental Station at Pittsburgh, Pennsylvania, through the courtesy of H. M. Cooper, supervising chemist of the Coal Analysis Section, is cooperating in this work by making analyses of the organic content of the sediments.

A preliminary examination of 12 long cores distributed representatively throughout the off-shore waters of the Gulf shows two distinctly different layers of sediment: (1) an upper zone of globigerina ooze, rich in calcium carbonate, 5–50 cm. in thickness, and (2) a lower zone of alternating bands of clay and extremely well-sorted, fine-grained silt, relatively poor in calcium carbonate. Although in a few places the two zones are separated by a layer of red clay or red mud of intermediate calcium carbonate content, in most cores the transition from alternating clay and silt to globigerina ooze is fairly abrupt. Cores from the area off the Rio Grande contain a few centimeters of foraminiferal ooze at the top, below which is fine silt extending to the bottom of the core. No alternating bands of clay and well-sorted silt have been noted in this area.

The lower zone of banded clay found throughout most of the Gulf consists of alternating layers of clay, 1 mm. to 30 cm. thick, and of silt, 0.2 mm. to 5 cm. in thickness. Most of the clay bands are 1–2 cm. thick; most of the silt bands, less than 1 mm. The silt is so well sorted that under a high-power binocular microscope it has the appearance of ordinary beach sand. Its average (median) diameter is estimated to range between 10 and 20 μ. Such good sorting in such a fine silt is most unusual.

Well-defined cross-bedding was noted in two cores: one, at a depth of 170 cm. beneath the sea floor in a sample taken from a sea mount near the edge of the con-

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[1] The authors are associated with the U. S. Geological Survey, Washington, D. C., Amherst College, Amherst, Massachusetts, and the Museum of Comparative Zoology, Cambridge, Massachusetts, respectively.

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tinental platform, and the other, 50 cm. beneath the sea floor in the abyssal deep near the edge of the continental slope off Campeche bank, north of the Yucatan peninsula. In the sample from the deep off Campeche bank, the false-bedded zone is 5 cm. thick, individual layers dipping up to 15°. The core there was not deformed, and the attitude of the bedding must be regarded as genuine.

One core (No. 143), taken in 3,546 m. of water in the middle of the Sigsbee deep in the deepest part of the Gulf, has been examined for Foraminifera. The upper foraminiferal zone, 50 cm. in thickness, is characterized by a subtropical planktonic fauna, dominated by *Globigerinoides rubra*, *Globorotalia menardii*, *G. tumida*, G. *truncatulinoides*, and *Pulleniatina obliquilata*. Between depths of 50 and 68 cm., in a zone of red clay or red mud, the fauna is transitional between cold- and warm-water forms. Between depths of 74 and 78.5 cm., at the top of the zone of banded clay and silt, the fauna is definitely sub-Arctic and is dominated by *Globigerina bulloides*, *G. pachyderma*, and small specimens of *Globigerinoides rubra*. Between 78.5 and 125 cm., the fauna is cold-water in type but is warmer than that between 74 and 78.5 cm.; and from 125 to 168 cm., at the bottom of the core, the fauna is definitely sub-Arctic. Abundant broken and seemingly eroded specimens were noted between 74 and 78.5 cm., 92 and 96 cm., and 113.5 and 116.5 cm.

A series of submerged hills rise above the sea floor near the outer edge of the continental platform, just inside the 100-fathom line, off the Louisiana coast between the Sabine and Atchafalaya Rivers. Two of these hills, lying within 10 fathoms of the surface, located in N. Lat. 27° 52.5′, W. Long. 93° 49′, and N. Lat. 27° 54.5′, W. Long. 93° 36′, were studied in some detail. The fathometer trace shows that they are remarkably flat on top and that they rise rather abruptly 300–400 feet above the surrounding muddy plain. On the side of one of these two hills the depth changed from 51 to 86 fathoms within a few ship lengths.

The sediments in these areas are influenced materially by the change in topography. The flat continental platform is underlain by sandy silt; the slopes of the hills, by silty, calcareous sand; and the tops, by round Lithothamnium balls and little or no sandy material. The Lithothamnium balls, dredged from water up to 20 fathoms in depth, have a maximum diameter of 10 cm. and seem to be alive on all sides, which suggests that they are rolled around by the waves or currents. In one place in 9 fathoms of water, several genera of corals, similar to common West Indian genera, were found with these balls.

The origin of these hills arouses speculation. Shepard (*2*) has suggested that they are salt domes. Trowbridge (*3*) also has noted calcareous sediments on the side of a "salt" dome on Southwest Pass. The distribution of sediments and the topographic relations, however, suggest bioherms or calcareous reefs described by Cummings and Shrock (*1*) from the Silurian of Indiana and Wisconsin. The hills perhaps may be erosional remnants, but, if so, either they must have been eroded prior to the deposition of the sandy silt forming the present continental platform or the hills protruded far enough above the surrounding flat, muddy plain to afford a place where calcareous organisms could live. The hills also conceivably could be associated with diastrophic deformation of the Gulf of Mexico basin.

The conditions of sedimentation obviously have changed profoundly in relatively recent geologic time. The upper zone of globigerina ooze, rich in calcium carbonate and characterized by a warm-water fauna, points to subtropical conditions similar to those now prevailing in the Gulf. The intermediate zone of red clay or red mud, noted in a few samples, is intermediate in carbonate content and contains a transition fauna between warm and cold. The lower zone, poor in calcium carbonate, and characterized by a cold fauna and alternating bands of clay and well-sorted silt, indicates the effect of the glacial epoch. The sediments in this bottom zone in general are essentially unchanged to the bottom of the deepest core, 250 cm. beneath the surface of the sea floor. Seemingly, therefore, only one major glacial epoch is represented.

The explanation of (1) the well-sorted, fine silt bands, (2) the layers of broken Foraminifera, and (3) the false bedding at depth in the cores offers a challenge to the imagination. Obviously, the water must have been in motion at the time of the development of the cross-bedding and also, perhaps, when the Foraminifera were broken. The false bedding, owing to the small dimensions of the core, conceivably could represent ripple marks, but, even if that is true, the bottom water must have been in motion to form ripples. How, then, could one account for deep movement of water according to prevailing notions of the sea—by tidal currents, internal waves, or deep currents? Roughness of the sea floor, just as roughness of land affects wind, must interfere with the movement of deep layers of water. But was the sea floor rough at the time of deposition of the false bedding? Perhaps the explanation lies (1) in lowering of the sea level because of removal of water during the ice age, (2) in submarine slumping, or (3) in recent deformation of the floor of the Gulf. The presence of the numerous well-sorted silt layers 200–300 miles from the present shore poses a real problem of transport. It is possible that these layers resulted from eolian action in the final stages of the ice epoch, when so much loess was being deposited. They also might have been laid down near shore. If so, our ideas of the magnitude of ocean changes in the late Pleistocene are likely to be materially different from those we have held in the past.

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Report of the year 1946

THE
WOODS HOLE OCEANOGRAPHIC
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REPORT FOR THE YEAR
1946

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Alexander Forbes, 610 Harland Street, Milton, Mass.
Ross G. Harrison, Yale University, New Haven, Conn.
A. G. Huntsman, University of Toronto, Toronto, Canada.
Columbus O'D. Iselin, Woods Hole Oceanographic Institution, Woods Hole, Mass.
Frank B. Jewett, 195 Broadway, New York, N. Y.
Lamar R. Leahy, 910 Park Avenue, New York, N. Y.
Frank R. Lillie, 5801 Kenwood Avenue, Chicago, Ill.
Alfred L. Loomis, Tuxedo Park, N. Y.
Daniel Merriman, Bingham Oceanographic Laboratory, Yale University, New Haven, Connecticut.
Albert E. Parr, American Museum of Natural History, New York, N. Y.
Alfred C. Redfield, Woods Hole Oceanographic Institution, Woods Hole, Mass.
Lawrason Riggs, 120 Broadway, New York, N. Y.
Elihu Root, Jr., 31 Nassau Street, New York, N. Y.
Lyman Spitzer, Jr., Yale Observatory, New Haven, Conn.
Harlow Shapley, Harvard University, Cambridge, Mass.
Henry L. Shattuck, 50 Federal Street, Boston, Mass.
Edward H. Smith, Third Coast Guard District Headquarters, 42 Broadway, New York, New York.
Selman A. Waksman, New Jersey Agricultural Experiment Station, New Brunswick, New Jersey.

III. REPORT OF THE TREASURER

To the Members and the Trustees of the
Woods Hole Oceanographic Institution:

Gentlemen:

The Accounts for the year 1946 have been audited by Messrs. Seamans, Stetson & Tuttle, certified public accountants of Boston.

During the year bonds costing $106,878.90 were redeemed at a net profit of $4,669.85 to which must be added $285.09, the applicable reserve for amortization, and stocks costing $97,614.92 were sold at a loss of $13,169.74, making a total realized loss for the year in the Endowment Fund of $8,214.80. The accumulated net gain on securities sold or redeemed is $95,443.53.

During the year $205,542.20 was invested in bonds and $95,395.70 in stocks, leaving $5,283.29 uninvested at the end of the year.

The amount due from General Funds to Special Income Account rose during the year from $37,094.76 to $44,113.51. The continued withholding of these funds due Special Income Account is due to the continued use of all available funds to finance Government contracts.

The net amount due from the Government including some items not invoiced and less excess allowance for overhead amounted to $393,484.26.

There was spent directly for the Government $793,899.92 in addition to which there was allowed for overhead including fixed allowances $207,758.76.

The fund for Periodic Replacements at the beginning of the year stood at $40,200.00 in book value of securities and cash of $24,548.26 (including $14,400.00 due from Current Funds Cash), or a total of $64,748.26. During the year the cost of the installation of the new engine on "Atlantis" amounting to $39,212.22 was charged to this fund, which with the other credits and debits reduced the fund to $31,483.94, consisting of bonds of the book value of $49,863.12 (market $50,727.50) and a cash deficit of $18,379.18, leaving the fund with a book value of $31,483.94.

The total income of the Institution from its Endowment Fund including special income, after the payment of Custodian Fees was $121,482.89. This is over $4,500.00 more than in 1945 and over $10,000.00 more than in 1944. This increase is due to greater return from some 28 stocks, and the collection of arrears on Commonwealth & Southern Preferred.

The net Institutional expenses amounted to $116,209.76, leaving a balance of $5,273.13 before transfer of special income of $7,018.75 to the Special Income Account.

Our cash position has improved slightly. Bank loans have been decreased from $360,000.00 to $330,000.00 and accounts payable from $53,310.80 to $47,613.45, and our current cash funds have risen from a deficit of $4,075.57 to a net balance of $27,319.03.

The additions to Plant Account more than offset the decrease in Current Surplus.

Our entire surplus and $330,000.00 of bank loans are still involved in the financing of the Government contracts.

The return on the investments held at the end of the year was at the rate of 4.52%. This is the rate after excluding dividends paid in stock and after taking into account the amortization of the premiums paid on bonds purchased above par.

At the end of the year the securities in the Endowment Fund had a market value of $2,826,349.07 which is $316,768.87 in excess of cost.

The Balance Sheet and the Statement of Income and Expenses are appended.

Respectfully submitted,

Lawrason Riggs
Treasurer

BALANCE — SHEET

As of December 31, 1946

ENDOWMENT FUND ASSETS

	Quoted Market Value		
Endowment Fund Assets:			
Bonds (less reserve for amortization of bond premiums, $3,631.47)	$1,084,311.57	$1,072,392.80	
Stocks	1,742,037.50	1,437,187.40	
Cash		5,283.29	$2,514,863.49

Note: Bonds having a book value of $483,145.17, are specificially allocated as collateral on the Institution's indebtedness to the Bankers Trust Company.

Reserve Fund Assets:			
Bonds	$14,225.00	$14,032.75	
Stocks	14,295.75	19,099.02	
Cash		1,234.87	34,366.64
			$2,549,230.13

PLANT ASSETS

Laboratory Plant:			
Land		$27,072.32	
Buildings		332,202.26	
Laboratory equipment		21,361.93	
Library		16,700.00	$397,336.51
Ketch "Atlantis":			
Construction		$218,674.47	
Equipment		27,298.50	
		$245,972.97	
Power Boat "Balanus"		46,043.29	
Power Boat "Anton Dohrn"		17,145.67	
Small Boats and Equipment		10,028.85	319,190.78
Hall Property, Land and Buildings			26,500.00
			$743,027.29
Depreciation Fund Assets (for Periodic Replacements):			
Bonds	$50,727.50	$49,863.12	
Cash (including $20,012.22 due Current Funds cash)		(18,379.18)	31,483.94
			$774,511.23

BALANCE — SHEET

As of December 31, 1946

ENDOWMENT FUNDS

Endowment Fund — General	$2,000,000.00	
Endowment Fund — for Upkeep of Plant	419,419.96	
	$2,419,419.96	
Add accumulated net gain on securities called or sold	95,443.53	$2,514,863.49
Reserve Fund	$23,658.07	
Add accumulated Reserve Fund Income	10,708.57	34,366.64
		$2,549,230.13

PLANT FUNDS

Plant Fund — General			$607,642.13	
Plant Fund Reserve — Transferred in prior years from Current Surplus		$ 88,949.87		
Add appropriation from Current Funds, Hall Property	$26,500.00			
Power Boat “Balanus”	46,043.29			
Library Additions	800.00	73,343.29		
		$162,293.16		
Deduct				
Sale of “Physalia”	23,408.00			
Sale of “Little Reliance”	3,500.00	26,908.00	135,385.16	$743.027.29
Reserve for Periodic Replacements				31,483.94
				$774,511.23

BALANCE — SHEET

As of December 31, 1946

(Concluded)

CURRENT ASSETS

Current Funds Cash:			
Main Account	$32,645.33		
Operating Accounts	16,860.52		
Petty Cash Funds	1,914,47	$51,420.32	
Less,			
Amount due Special Income Fund	$44,113.51		
Amount due from Depreciation Fund	(20,012.22)	24,101.29	$27,319.03
Special Income Assets:			
Investments			
Bonds (quoted market value $9,728.75)	$9,739,31		
Stocks (quoted market value $7,741.75)	6,196.60	$15,935.91	
Cash (including $44,113.51 due from Current Funds Cash)		44,568.21	60,504.12
Accounts — Receivable:			
United States Government Contracts,			
Invoiced on public vouchers	$169,060.53		
Invoiced after December 31, 1946	182,749.70		
Expenditures not invoiced	58,635.57	$410,445.80	
Less allowance for Overhead and Boat Costs collected in excess of charges		16,961.54	
		$393,484.26	
Advances to be repaid		7,650.89	
Sundry		4,204.23	405,339.38
Supplies in Stock			10,186.40
Deferred Charges to Government Allowance			1,117.97
			$504,466.90

BALANCE — SHEET

As of December 31, 1946

(Concluded)

CURRENT LIABILITIES AND SURPLUS

Accounts — Payable:			
Institution		$2,082.51	
United States Government contracts		39,529.24	
Income Taxes withheld		6,001.70	$47,613.45
Notes — Payable (secured by bonds having a book value of $485,145.17)			330,000.00
Unexpended Grants:			
Wallace and Tiernan Gift			1,199.36
Surplus:			
Balance at December 31, 1945		$163,424.20	
Add			
Excess of Income over Expenditures for the year ended December 31, 1946		5,273.13	
Book Value "Physalia" sold	$23,408.00		
Gain on sale	2,842.00	26,250.00	
Book Value "Little Reliance" sold	$3,500.00		
Gain on sale	500.00	4,000.00	
Gain on sale Special Income Investment		50.05	
		$198,997.38	
Deduct cost of Plant Assets purchased from Current Funds,			
Hall Property	$26,500.00		
Power Boat "Balanus"	46,043.29		
Additions to Library	800.00	73,343.29	125,654.09
			$504,466.90

Income from Endowment Fund and Special Income Investments and Expenditures Applicable Thereto

Year ended December 31, 1946

INCOME:			
From Endowment Funds,			
Interest	$40,400.42		
Dividends	82,390.77		
From Special Income Securities	516.39	$123,307.58	
Less Custodian Fees and Expense		1,824.69	
Total Income			$121,482.89
INSTITUTION EXPENSES:			
Upkeep of Plant,			
Depreciation	$4,800.00		
Buildings and Grounds	1,361.69	$6,161.69	
Operating Expenses,			
Scientific Salaries	$44,466.62		
Scientific Projects	30,947.49		
Scientific Supplies and Expense	3,772.04		
Publications	2,069.26		
Contributions to Retirement Fund	1,763.26		
Travelling Expense	1,650.69		
Amortization of Bond Premiums	1,358.68		
Grants and Fellowships	210.79		
Administration	738.69		
Expenses of Hall Property	142.32		
	$87,119.84		
Less Sundry Credits	2,352.72	84,767.12	
Institution Overhead		25,280.95	
Total Expenditures			116,209.76
Excess of Income			$5,273.13

IV. REPORT OF THE DIRECTOR

By C. O'D. ISELIN

Introduction

During 1946 the activity, both in the laboratory and at sea, remained at a high level. The Government requests for oceanographic information, personnel and equipment were undiminished and at the same time a small beginning was made on the part of our permanent staff to develop the Institution's own post-war program. It was possible to operate on this expanded scale because several former members of our staff returned from serving in the Armed Forces and also we were able to find a number of new people who in one way or another were qualified to take part in the program required by the various contracts with the Government.

The chief reason for this rather unexpected, continuing activity was the opportunity afforded by the atomic bomb tests at Bikini Atoll for conducting various types of oceanographic investigations. More than 40 members of our staff took part in the many phases of this unique experiment.

Although much equipment and a considerable fraction of our staff were in this way diverted to the middle of the Pacific Ocean, field work was also active in the Atlantic. This was made possible through two new contracts with the Government, both of which required the use of our vessels in surveys of the distribution of temperature and salinity over considerable areas. As a result of these operations it has become evident that postwar costs of oceanographic field work have more than doubled as compared with the period just before the war. This is perhaps the most serious problem facing the Institution today. The costs of operating our own vessels have become so high that without Government subsidy we could not hope to undertake offshore observations. For the time being, at any rate, the Government is able to support science at private laboratories on an unprecedented scale, but should we have to return to operating solely on income from endowment, we could no longer afford more than a small program of field observations in local waters.

This unhappy situation has very much influenced the operations of the past year and has delayed the resumption of a balanced research program in which the analysis and publication of results keeps pace with the collection of new data. Facing the prospects of a greatly reduced field program within the next year or two, we have deliberately exerted every effort to keep our vessels busy accumulating observations. As a result, we have only a relatively small output of scientific publications to point to after an extremely busy year.

The Facilities at Woods Hole

A serious limiting factor during the past year has been the shortage of housing and laboratory space at Woods Hole. During the winter months, as in the past several years, we were able to expand into the Marine Biological Laboratory, but when summer came and an unexpected number of biologists returned to Woods Hole the situation became acute. It was not until autumn, when several members of our staff left to take up university positions, that the pressure was relieved. Although our administration staff, in cooperation with the Marine Biological Laboratory, had made every effort to provide accommodations for the expected number of summer visitors, the carefully laid plans were upset when late in the spring more and more people decided to come to Woods Hole. As far as laboratory space is concerned, it will be an easy matter in the future to avoid the mistakes of the past summer. We will not again plan on using any of the facilities of the Marine Biological Laboratory during the summer, but it will be some time before the living accommodations at Woods Hole can equal the combined demands of both laboratories.

Through the cooperation of the U. S. Fish and Wild Life Service, the housing shortage has been somewhat lessened during the past year, for the former residence building has provided accommodations for about 35 people. Nevertheless, it is evident that much new construction will be required.

The Marine Biological Laboratory has continued to make available to us the former Penzance Garage. Thus wharfage, storage space, machine shop space and the parking of automobiles have been no serious problem. However, this is a commercially valuable piece of property and commands a high rental. If oceanography is to be continued on anything like the present scale at Woods Hole, in the long run a less expensive solution to the storage problem will have to be found.

As a step in this direction in October the Executive Committee authorized the purchase of some property almost directly across the street from our main building. The tract has a street frontage of 42 feet and extends back to the Eel Pond for approximately 117 feet. Due to irregular widening along the northwestern property line, the Eel Pond frontage is about 50 feet. The land now has three small buildings on it which are fully rented and therefore it can be carried without loss of income. However, before undertaking any new construction, either for living accommodations, laboratory space, or storage, it will be wise to wait until the future activity can be gauged with some assurance.

Vessels

The following is a summary of the cruises made by "Atlantis" during the past year:

Cruise No.	Date	Region
138	Jan. 3–6, 1946	South of No Mans Land.
139	Jan. 30–31,	New London to Woods Hole.
140	Feb. 6–May 9	Woods Hole to Guantanamo to Miami to Woods Hole.
141	May 22–30	Woods Hole to Gulf Stream off Hatteras to 64° W.
142	June 3–7	Woods Hole to south off continental shelf.
143	Sept. 16–Nov. 16	Woods Hole to Bermuda, two runs south to Antilles and return to Woods Hole.

During the winter months, while operating off Guantanamo, it became evident that the main engine should soon be either replaced or completely rebuilt. After 15 years of hard service, this was, of course, no great surprise. The various alternatives were carefully considered in consultation with representatives of the Bureau of Ships of the Navy Department. Since "Atlantis" is the only vessel in this country which from the outset was designed with oceanography as the primary purpose, the Navy has a special interest in her continued efficient operation. Thus it was decided to make available a surplus engine of far greater horsepower and quality than the Institution itself could ever have considered. With the Government furnishing the machinery, the funds which the Institution had been accumulating for the expected rebuilding of the original engines could be used for a complete rearrangement of the engine room, including a new forced hot water heating system. The new installations were made by the Electric Boat Company of Groton, Connecticut, during July and August. As a result the "Atlantis" is now far better equipped with propelling and generating machinery than when she was new. The main engine can deliver 350 horsepower to the original feathering propeller. Thus we have retained the important feature of being able to tow nets at very low speeds. Cruising speed has been increased from about 7 knots to 9 knots without any serious loss in cruising radius. At the same time, we have ample reserve power to maintain speed when bucking a head sea. Two separate generating sets of 30 and 35 K.W. capacity provide ample direct current. The relatively small amount of alternating current required is supplied by converters.

In September, Captain Adrian K. Lane took over command of "Atlantis" from Captain Gilbert Oakley, Jr. The latter then assumed responsibility for the operation and maintenance of all our vessels, as well as the other duties which had been so ably carried out by Mr. John D. W. Churchill during the war period.

In July the opportunity arose to sell the "Physalia" which was somewhat light for offshore work, having been originally designed as a yacht. At the same time and at very nearly the same price, we were able to purchase a fishing type vessel originally built in 1942 but turned over to the Army before she was outfitted for fishing. The new vessel has been named "Balanus". Following use during the summer in geophysical work, we have begun to fit her out for general oceanography. The "Balanus," of 42 net tons, has a heavily constructed wooden hull, 72 feet in length. A heavy duty diesel engine of 155 horsepower enables her to cruise at 8.5 knots. She carries a crew of 8 and has additional accommodations for a scientific party of 5.

The smaller vessels owned by the Institution are now the "Asterias" and the "Mytilus," the "Little Reliance" having been sold last spring.

The remainder of the fleet are the "Mentor," which we now maintain and will later operate for the Bureau of Ships, and the Schooner "Reliance" and the "Claire," which are also Government owned and which are used for the work being carried out under contract with the Bureau of Ordnance.

The "Mentor," a 127 foot converted yacht which has been especially fitted out for acoustical research, was operated until July by a Navy crew. Because of greater horsepower and much more elaborate electronics installations, she will require a slightly larger civilian crew than "Atlantis." In assuming the responsibility for the maintenance and operation of the "Mentor," we have taken a new step which constitutes a rather crucial experiment for oceanography. More and more the facilities and instrumentation needed in the earth sciences are owned by the Government. Does this mean that the private laboratories will gradually give way to the Government laboratories because they cannot afford the elaborate new equipment? I believe that so specialized a vessel as the "Mentor" can be more efficiently operated by a civilian crew than by a Navy crew and events seem to indicate that the Navy has sufficient confidence in the Institution to give this plan a try. Should we fail in this responsibility, then it seems likely that the Government will of necessity seek other means of developing the earth sciences. Surely the Government as the only agency now capable financially, must encourage, in one way or another, continued development of the earth sciences. Unless man continues to broaden his knowledge of the earth, including the oceans, he will not be able to develop fully the potential resources of his environment.

Personnel

There have been many changes in personnel during the past year. This was to be expected as people were released by the Armed Services and as the universities resumed full scale operations. It will be only possible to record a few of these changes here which for one reason or another seem particularly notable.

Former staff members and scientific workers returning from the Armed Services include: Mr. Gilbert Oakley, Jr., Dr. H. R. Seiwell, Dr. Mary Sears, Mr. L. Valentine Worthington, and Mr. Martin J. Pollak.

Scientists and technicians who have for the first time been employed here and who served in the Army or Navy during the war are: Dr. J. Brackett Hersey, Mr. John F. Holmes, Mr. Leslie Carter and Mr. Andrew F. Bunker.

In July Dr. Jeffries Wyman returned to Harvard University to resume full time duty in the Department of Biology. Mr. David M. Pratt and Dr. W. T. Edmondson also now have teaching positions in biology at Harvard.

Early in the year Dr. Paul C. Cross left to become Chairman of the Department of Chemistry at Brown University. In the autumn, Dr. J. S. Coles became Assistant Professor in his Department. On the other hand, Dr. Norris W. Rakestraw left Brown University and his part time position on our staff for the Scripps Institution of Oceanography. His title there is Professor of Oceanography, University of California at Los Angeles.

Last winter Dr. Wm. M. Ewing took up his new duties in the Geological Department of Columbia University. Mr. J. Lamar Worzel and Mr. Nelson C. Steenland are at present doing graduate work under his supervision.

Dr. Edward S. Deevey, Jr., returned to Yale University as Lecturer in Biology. Dr. Gordon A. Riley has been appointed Assistant Professor, a part time position, at Bingham Oceanographic Laboratory, Yale University.

Dr. Robert H. Cole has gone to the University of Missouri and Dr. Leonard L. Liebermann to the Marine Physical Laboratory at San Diego. Mr. Thomas S. Austin and Dr. Clifford A. Barnes have taken positions in the Division of Oceanography, Hydrographic Office.

Mr. Henry C. Stetson and Mr. William E. Schevill have resumed half time duty at the Museum of Comparative Zoology. Mr. Gardner Emmons has likewise returned to New York University.

Fellowships

The following were awarded fellowships by the Institution during the past year: Miss Margaret Briggs, Mr. William S. Butcher, Dr. Shu-ping Chu, Dr. James Lackey, Dr. Hans A. Panofsky, Mr. George Whiteley, Jr., and Mr. Nelson C. Steenland.

Visiting Investigators

Dr. Hilary B. Moore, Resident Naturalist at the Bermuda Biological Station, came to Woods Hole in October for an extended visit. Somewhat shorter visits were made by Dr. Walter Munk and Mr. Walter Champion of the Scripps Institution of Oceanography.

Visitors from abroad who spent some time at the Laboratory included the following: Dr. J. N. Carruthers of the British Hydrographic Office, Oceanographic Section; Dr. Johan Ruud, Professor of Marine Biology at the University of Oslo and Dr. Hamed Abdul Fattah Gohar, Director of the Marine Biological Station at Ghardaqa, Egypt.

Library

Our contribution towards the purchase of new books and periodicals at the Library of the Marine Biological Laboratory has continued to be at the rate of $800.00 per year. However, by mutual agreement, our contribution towards the operating expenses of the Library has been substantially increased.

Publications

One number of Papers in Physical Oceanography and Meteorology, Vol. 10, No. 1, appeared before the end of the year.

Dr. Sears has spent considerable time reorganizing the mailing list for Institution publications and reestablishing contact with exchanges abroad from whom we have been cut off during the war years.

The complete list of numbered contributions for the year **1946** [redacted] is as follows:

No. 301. F. G. Walton Smith. Effect of Water Currents upon the Attachment and Growth of Barnacles. *Biol. Bull.* Vol. 90, No. 1, pp. 51–70.

No. 341. Nelson Marshall. Observations on the Comparative Ecology and Life History of two Sea Robins, *Prionotus carolinus* and *Prionotus evolans strigatus*. *Copeia* No. 3, pp. 118–144.

No. 342. John D. Ferry and Dayton E. Carritt. Action of Antifouling Paints: I. Solubility and Rate of Solution of Cuprous Oxide in Sea Water. *Industrial and Engineering Chemistry* Vol. 38, pp. 612–617.

No. 343. M. Juul Hvorslev and Henry C. Stetson. Free-Fall Coring Tube: A New Type of Gravity Bottom Sampler. *Bull. Geol. Soc. Amer.* Vol. 57, pp. 935–950.

No. 344. Fred B Phleger, Jr., and Walter A. Hamilton. Foraminifera of two Submarine Cores from the North Atlantic Basin. *Bull. Geol. Soc. Amer.* Vol. 57, pp. 951–966.

No. 345. John D. Ferry and Gordon A. Riley. Action of Antifouling Paints: II. Solubilities of Antifouling Toxics in Sea Water. *Industrial and Engineering Chemistry.* Vol. 38, pp. 699–701.

No. 346. John D. Ferry and Bostwick H. Ketchum. Action of Antifouling Paints: III. Maintenance of the Leaching Rate of Antifouling Paints Formulated with Insoluble, Impermeable Matrices. *Industrial and Engineering Chemistry.* Vol. 38, pp. 806–810.

No. 347. Bostwick H. Ketchum, John D. Ferry and Arthur E. Burns, Jr., Action of Antifouling Paints: IV. Maintenance of Leaching Rate of Antifouling Paints Formulated with Soluble Matrices. *Industrial and Engineering Chemistry*, Vol. 38, pp. 931–936.

No 348. Maurice Ewing, Allyn Vine and J. L Worzel. Photography of the Ocean Bottom. *Journ. Optical Soc. Amer.*, Vol. 36, No. 6, pp. 307–321.

No. 349. C. M. Pomerat and C. M. Weiss. The Influence of Texture and Composition of Surface on the Attachment of Sedentary Marine Organisms. *Biol. Bull.*, Vol. 91, No. 1, pp. 57–65.

No. 350. Marshall Schalk. A Study of Textural Changes in a Beach by repeated Samplings. *Journ. Sedimentary Petrology*, Vol. 16, No. 2, pp. 43–51.

No. 351. Maurice Ewing, G. P. Woollard, A. C. Vine and J. L. Worzel. Recent Results in Submarine Geophysics. *Bull. Geol. Soc. Amer.*, Vol. 57, pp. 909–934.

No. 352. G. A. Riley and D. F. Bumpus. Phytoplankton-Zooplankton Relationships on Georges Bank. *Sears Found. Journ. Marine Res.*, Vol. 6, No. 1, pp. 33–47.

No. 353. G. A. Riley. Factors Controlling Phytoplankton Populations on Georges Bank. *Sears Found. Journ. Marine Res.*, Vol. 6, No. 1, pp. 54–73.

No. 354. H. R. Seiwell. Military Oceanography in Tactical Operations of World War II. *Trans. Amer. Geophysical Union*, Vol. 27, No. 5, pp. 677–681.

No. 362. Richard A. Craig. Measurements of Temperature and Humidity in the Lowest 1000 feet of the Atmosphere over Massachusetts Bay. *Papers in Physical Oceanography and Meteorology*, Vol. 10, No. 1, pp. 1-47.

No. 363. George L. Clarke. Dynamics of Production in a Marine Area. *Ecological Monographs*, Vol. 16, No. 4, pp. 322–335.

Scientific Program

Under the present circumstances when so large a percentage of the activity of the laboratory is being financed under contract with the Government, it is most difficult to separate the investigations for which the Institution is primarily responsible from those which are largely or entirely undertaken at the request of the Government. Although we have set up an accounting system which permits the costs to be rather rigidly separated, the two programs are in many cases so closely integrated that it is difficult to describe them separately. In the following list, the emphasis gradually changes from studies which are entirely our own to those which are entirely for the Government. However, applications of oceanography developed for the Government will not be stressed. It will be seen that as time goes on our definition of oceanography is gradually being expanded to include almost all that goes on in, under, and above the sea.

1. The Productivity of the Sea.

Prior to the war, this was the central subject of investigation by the biologists and chemists of the Institution. The recent advances in the subject have been summarized by Dr. H. W. Harvey of the Plymouth Laboratory in a small book published in 1945. It is gratifying to see from this review what a substantial contribution to the subject as a whole has come from Woods Hole.

In resuming studies of the productivity of the sea, the chief objective will be the measurement of the factors underlying the productivity of coastal waters. Drs. George L. Clarke and W. T. Edmondson have undertaken, with the collaboration of others, the investigation of semi-enclosed arms of the sea and salt ponds where more detailed and precise measurements can be conducted than offshore and where changes in the physical and biological components can be followed closely.

Systematic studies have been made during the year in Tisbury Great Pond, (Marthas Vineyard), Rand Harbor at Megansett and Little Harbor, Cohassett, (Massachusetts). These have included tests of the addition of chemical fertilizer to the water in situations where the exchange of water could be controlled or limited. Results showed that biological activity could be greatly increased by such treatments.

To facilitate further studies on productivity, two concrete tanks supplied with sea water from the harbor were constructed outside the laboratory building. The tanks are 9 by 18 by 5 feet deep and protected by a glass roof. Tests in these tanks may be conducted efficiently under more natural conditions than exist in the laboratory but without the complicating effect of interchange with bottom muds. Large populations of phytoplankton were readily produced in the tanks when fertilizers were added.

Dr. H. H. Haskin, now of Rutgers University, conducted a number of surveys of the chemical conditions in the sea water overlying the oyster beds of Gardiners Bay, (Long Island, New York). His object is to determine the nutritional conditions responsible for the unusual value of this area for the cultivation of oysters.

2. Studies of the Pollution of Sea Water.

The distribution and extent of bacterial pollution of sea water depends upon the source and method of disposal of sewage, the local hydrographic conditions and the viability of the bacteria involved. Several aspects of a complete investigation of these problems have been initiated.

Several trips were made to Mount Hope Bay, where the hydrographic conditions were being explored. The distribution of pollution bacteria was closely correlated with the water circulation at various stages of the tide. With the aid of Mr. Amos Hopkins, a survey of pollution of Woods Hole was made. Continuation of these studies as the local sewerage system is installed will demonstrate the effectiveness of the system.

Dr. Cornelia Carey and Miss Margaret Briggs have started an investigation into the factors controlling the viability of coliform bacteria in the sea. Sea water has been found to contain a substance destroyed by autoclaving, but not by boiling for a few minutes. This substance is lethal for the strain of *Escherichia coli* used. The seasonal variation in the potency of this substance and its distribution in water collected from various locations is being studied along with the effect of aging the water in the laboratory. In addition, it has been observed that certain bacteria in raw sea water are able to prevent the development of coliforms on nutrient agar plates in their immediate vicinity. It seems probable that these forms are secreting an antibiotic substance which may be important in the rapid reduction of the bacterial pollution of sea water.

3. The Biology of Fouling Organisms.

The group of biologists who were engaged in work on the prevention of fouling during the war have been winding up that work and continuing parts which have more general scientific interest. The final assignment from the Bureau of Ships was to prepare a comprehensive book reviewing all existing knowledge of fouling. The parts of this book dealing with the general biology of fouling organisms have been completed, and the chapters covering the practical methods of preventing fouling, previously issued, have been revised, so that the final manuscript will soon be ready for the press.

A very extensive collection of samples of fouling from navigation buoys from all parts of the coast of the United States was made during the war. The immediate study of this material was directed toward obtaining the answers of certain special questions of interest in mine warfare. The material, however, is of unique interest in connection with the geographical distribution of marine organisms along the coasts. The collections have been sorted with reference to the several different classes of animals or plants, and have been submitted to specialists on the various groups for identification and study. This work involves cooperation with experts connected with Yale University, the Bingham Oceanographic Laboratory, the Museum of Comparative Zoology, the University of California, the University of Oregon, Rhode Island State College and the Texas Game, Fish and Oyster Commission.

Six papers dealing with special aspects of the fouling problem were published during the year and a number of others were prepared for publication. Dr. Alfred C. Redfield was asked to organize a Symposium on Marine Ecology, which was presented before the Ecological and Limnological Societies at the Boston Meeting of the A.A.A.S. Two members of our staff, Drs. Bostwick H. Ketchum and Louis W. Hutchins, took part in the program

4. Geophysics of the Continental Shelves.

During the summer, Dr. Maurice Ewing, Dr. George P. Woollard, Mr. J. Frank Press, Mr. Nelson Steenland and Mr. J. Lamar Worzel continued their work on the geophysics of the continental shelves under a Geological Society of America grant. Using improved technique and instrumentation as compared with their pre-war work, they occupied 15 stations between the Gulf of Maine and the region off Cape May, New Jersey. On three lines the seaward slope of the older crystalline rocks was mapped beneath the veneer of younger (Cretaceous and Tertiary) sediments. Work in the Gulf of Maine was discontinued when these younger beds were found extremely thin or entirely lacking. To the south, with some local reversals, the wedge of sediments was found to thicken markedly, the maximum thickness reached exceeding 17,000 feet. The southern-most line indicated that their original work off Norfolk, generally discredited at the time it was made, was reasonable in showing a thickness of some 12,000 feet of sediments. The oil test well drilled during the year on Cape Hatteras further substantiated their original conclusions.

5. Distribution of Marine Sediments.

During 1946 sedimentary work was continued by a study for the Navy of that part of the Gulf of Maine lying immediately off Portsmouth. Under the direction of Mr. H. C. Stetson, Dr. Fred B Phleger and Mr. David B. Ericson, about 700 bottom samples including several hundred short cores were taken. Most of the samples were taken by Mr. Ericson who also did the major part of the laboratory analysis. From study of these samples, charts have been made showing various characteristics of the sediments of the area.

Study of the cores proved that in the deeper parts of the Portsmouth basin, three distinct layers of sediments occur. The oldest, glacial till devoid of organic remains, is overlaid by mud and silt containing sponge spicules, diatoms and calcareous foraminifera, which distinguish it from the third and uppermost layer of mud and silt containing the arenaceous foraminiferal fauna now living on the bottom of the basin.

Preliminary mechanical analyses of the post-glacial beds show that the average particle diameter of the older layer is about twenty percent finer than that of the material being deposited at present. That the older bed with its calcareous fauna is the seaward extension of the post-glacial marine clays of Maine, New Hampshire and northern Massachusetts, appears to be well established by its stratigraphic position directly above the till and by its smaller particle diameter implying deposition in deeper water.

From the degree of tilting of the land mass as determined by present elevations of deltas built into the marine clays, it is inferred that the uplift of the floor of the Portsmouth basin must have been in the order of 50 meters. Depth of water over Jeffreys Ledge before tilting would then have been about 70 percent deeper than now. A connection between the faunal change and the shoaling of water over Jeffreys Ledge appears probable since the ecological conditions in the Portsmouth basin must in large measure be determined by the extent to which the ledge acts as a barrier to the circulation of water in and out of the basin. The problem deserves further study, particularly investigation of the foraminiferal faunas occurring in deeper water seaward from Jeffreys Ledge.

6. Hydrography of the Western North Atlantic.

During the past year a good beginning was made in a broad new attack on the problems of circulation, and of the distribution of temperature and salinity in the Western North Atlantic. Such studies constituted the major effort of the Institution before the war, and it is now clear that because of new instrumentation and methods, the work can be resumed with excellent prospects of success. Adequate facilities for analyzing large numbers of observations and financial support for a continuing field program have been assured through a new contract with the Office of Naval Research. This contract is under the technical supervision of the Division of Oceanography of the Hydrographic Office.

The field program consisted of monthly surveys of two selected areas near the coast, and of less frequent surveys of the waters over the continental shelf and along the northern edge of the Gulf Stream. Beginning in September, the "Atlantis" began a systematic survey of the whole, roughly triangular, area between Cape Hatteras, Bermuda and Puerto Rico. By the end of the year, four north-south profiles of deep hydrographic stations had been completed in the eastern part of this area.

Mr. Frederick Fuglister has been in charge of the routine processing and analysis of the very large number of bathythermograph observations secured in the course of this work. Mr. Dean Bumpus directed the field work in the coastal waters, while Mr. Fuglister and Mr. Valentine Worthington alternated as scientist in charge of the off-shore surveys of "Atlantis". Mr. Martin J. Pollak, who like Mr. Worthington has recently returned from service in the Navy, has had the responsibility of working up the deep hydrographic material.

The chief technical advance at sea has been the use of Loran. This new navigational method is of great importance to oceanography. Not only does it increase the accuracy of the location of stations, but it also makes it possible to obtain continuous information on the direction and velocity of the surface currents. Although an individual Loran fix may be in error by as much as a mile or two, when frequent fixes are obtained, for example, every half hour, the drift of the vessel due to currents can be determined with very satisfactory accuracy. By combining Loran with frequent bathythermograph lowerings, the "Atlantis" has also been able to track the northern edge of the Gulf Stream with most illuminating results.

In shallow waters, the new salinity recorder has likewise proved to be a very powerful tool. In this instrument, measurements of electrical conductivity and temperature are combined to produce a continuous record of salinity with an accuracy of about ±0.1 parts per thousand. While underway, the surface water can be circulated through the conductivity cell. On station, the cell can be lowered so as to produce a salinity-depth curve. In areas where relatively large changes in salinity are found, as off the mouth of a river, the salinity recorder is invaluable.

The fact that oceanographic vessels can now accumulate temperature and salinity observations, as well as surface current observations, without stopping not only greatly increases the volume of data to be analyzed in the laboratory, but also makes it advisable to institute new methods of analysis and new means of presenting the data for publication. Although the work has been pushed vigorously in the laboratory, the combining of the new observations with those accumulated before the war is by no means an easy task. Most of the recent observations are relatively shallow ones and show that the surface layer of the ocean has a complex and rapidly changing structure. To reconcile this complicated superficial layer with the rather simple permanent current patterns indicated by the pre-war, widely separated, deep hydrographic stations, one needs to have a much more detailed understanding of the eddy structure, both large and small, and of the local wind currents than is yet available. To resolve some of the problems may require the sort of three dimensional picture that can only be built up from the observations of several ships operating simultaneously in a relatively small area. In the meanwhile, from the relatively simple area south of the Gulf Stream, we are accumulating excellent statistical data on the seasonal and diurnal temperature cycles. The time is approaching when from this area, at least, we can begin to study annual variations in the temperature of the water column.

7. Marine Meteorology.

In the spring of 1946, an Institution group led by Dr. Jeffries Wyman and including Mr. Alfred H. Woodcock worked in the Trade Wind area on the exchanges of heat and water vapor between air and sea. The contract for this work was with the Bureau of Ships. Most of the observations were made about 100 miles northeast of San Juan, Puerto Rico, but in an area believed typical of the Trades. Observations were made by a relatively slow flying plane and included wet and dry bulb temperatures at accurately known heights, direct (although approximate) measurements of vertical velocities and high altitude photogrammetric study of cloud distribution. Ample bathythermograph observations gave information on the temperature structure of the surface waters. The trade wind air was found to consist of 3 distinct layers — the sub-cloud, cloud, and super-cloud. Except in the clouds, the roughest air, as shown by horizontal accelerometer traverses within each layer, was in the sub-cloud layer where it decreased with height. Temperature, humidity and lack of increase in roughness or turbulence directly beneath a cloud indicated that, unlike convective clouds over land, trade wind clouds originate primarily within the cloud layer rather than from surface warming of the air. Departure of the actual lapse rate within a cloud from the ideal moist adiabat served to indicate the amount of "outside" air entrained by the rising cloud. Surface solar measurements were analyzed with respect to bathythermograph data to calculate the total energy return from the sea.

Observations made during the war by the Radiation Laboratory (Massachusetts Institute of Technology) with Army and Navy cooperation were analyzed for the Bureau of Ships by Mr. Richard A. Craig and Mr. Gardner Emmons under the supervision of Dr. R. B. Montgomery. The observations consist primarily of vertical sounding through the lowest 500 meters of air over the ocean and are unique in regard to accuracy and detail. They reveal for the first time the types of vertical structure that occur in this part of the atmosphere. One group of 51 analyzed soundings was published, and a second group is in preparation.

Mr. Craig initiated a study to determine the distribution of eddy diffusivity on vertical atmospheric cross sections based on the soundings described above and he and Dr. Montgomery contributed to a conference on "Convection layers in the atmosphere and ocean" at The New York Academy of Sciences.

A study of the meteorological conditions leading to fog information is being carried out by Dr. Montgomery. The plan is to bring this subject up to date by applying the present knowledge regarding turbulent transfer and by incorporating results from the soundings described above.

A compilation of the latest determinations of the viscosity and other physical properties of air has been completed in preliminary form.

A study of the construction and use of the "Taylor characteristic diagram" in problems concerning the measurement and distribution of temperature and humidity at low levels was initiated.

Summer visitors included Dr. B. Haurwitz. Mr. H. A. Panofsky worked on an Institution Fellowship. During the fall, Mr. Woodcock spent some time in Florida measuring the amount and size of the salt particles in the air. In collaboration with Mr. Henry M. Stommel, he prepared a short paper on temperature gradients close to the surface of a small fresh water pond.

8. Development of Oceanographic Instruments.

During the past year, progress has been made mainly in two directions: wave recorder and wave period analyzer under the supervision of Mr. Arthur Klebba, and salinity-temperature-depth recorder under the supervision of Mr. Allyn Vine. Both of these developments have been financed through a contract with the Bureau of Ships, Navy Department.

With only minor interruptions, a bottom mounted, pressure type wave meter has been in operation off Cuttyhunk Island since early in 1946. Through the experience gained in operating at this station, the design was gradually improved and a second set of equipment built for installation at Bermuda. The "Atlantis" delivered the cable and the instruments to the Bermuda Biological Station in October and Mr. Frank Mather completed the installation about two weeks later. Unfortunately, the first cable used, which was light rubber covered cable known as demolition cable, soon developed leaks. In attempting to mend these, the cable was further damaged by the coral and the whole off-shore end finally had to be abandoned.

Mr. Mather returned to Woods Hole and made ready a slightly better quality cable which he laid from a small launch early in January 1947. The wave recorder has been operating successfully at Bermuda for over six months. Through these experiences, we have found that when proper precautions are taken, even on a rough and exposed coral bottom, inexpensive, small diameter, rubber covered cables will suffice. Thus the chief drawback of the pressure type wave meter, namely the expense of laying an armored cable, seems to have been overcome.

At Woods Hole, the records from both Cuttyhunk and Bermuda have been run through the wave period analyzer and Dr. H. R. Seiwell has undertaken the study of these data. It should perhaps be pointed out that the Bermuda records are unique in that the pressure unit is at the edge of the reef and records long period waves that have not yet been modified by moving across a continental shelf.

The salinity-temperature-depth recorder gives promise of becoming a relatively simple and inexpensive oceanographic instrument, although in its present form these virtues have clearly not yet been achieved. The sensitive element consists of a conductivity cell, a resistance type thermal unit and a pressure measuring device. These may be lowered on a multi-conductor cable connected to the recorder which is on board the vessel. Conductivity and temperature are combined electrically to give salinity. A study of how these circuits might be simplified is in progress; meanwhile, as mentioned above, the preliminary model has been undergoing tests at sea. An important feature of this instrument is that when used as a surface salinity recorder it enables the research vessel to track any given surface isohaline.

Mr. J. Lamar Worzel has been studying possible means of increasing the depth range of the bathythermograph. The practical depth limit of the present type of pressure element is about 300 meters. Two instruments, which have tested satisfactorily in the laboratory under pressures equivalent to 2000 meters, have been constructed, but it is too early to report on the success of repeated use at sea. In any such instrument, corrosion problems can be critical.

9. Pacific Ocean Biology.

A new project, "Pacific Ocean Biology", which started September 1, 1946 under contract with the Office of Naval Research, is a departure from the usual types of investigations conducted at the Institution. Admittedly, the need for increased knowledge of the Pacific area is great. At the same time, it is highly desirable that some central headquarters for information be established. The reasons for locating the project at Woods Hole include the excellence of the Marine Biological Laboratory library and the availability and interest in the project of a former Institution worker, Dr. Charles J. Fish. The latter's experience with the Navy in the Pacific and elsewhere plus his previous training makes him a logical person to supervise the work.

The objectives may be divided into two parts. The first is to assemble and analyze all available data on the zoöplankton, reef building corals, fouling organisms, phosphorescence and sound-producing marine animals. Material published in foreign languages is being carded, abstracted and translated as necessary and a complete bibliography assembled. Unpublished findings of various U. S. Government agencies and similar materials from other governments as available also serve as source material. The second part of the project, on completion of the analysis and survey of the field, is to prepare recommendations for such new work as may be necessary. Thus the Institution is for the first time directly concerning itself with a phase of oceanography definitely beyond the confines of the North Atlantic Ocean.

10. Underwater Acoustics.

Studies of the environmental factors influencing the transmission of sound in seawater have been continued throughout the year under a contract with the Bureau of Ships, Navy Department.

Transmission measurements at the higher frequencies were carried out from the USS "Mentor", a converted yacht acquired by the Navy and especially equipped for acoustical research. Dr. George P. Woollard directed the analyses of these data. A series of smaller scaled, and therefore more easily controlled, experiments were carried out in local waters under the supervision of Dr. Leonard Liebermann. Measurements of the reflectivity of the bottom and of the sea surface under a variety of conditions were obtained, as well as some determinations of the attenuation of sound by the decay method. Frequent breakdown and acute shortages of Navy personnel so hampered the operations of the "Mentor" that in August she was decommissioned. However, Dr. J. B. Hersey was able to carry out some much needed calibration studies while the ship was in operation.

The observations at much lower frequencies, secured during the previous year in the course of the experiments with Sofar, continued to be studied. Four men were trained in this new and most promising method of locating survivors at sea, and were sent out to the Pacific to help the Navy install receiving stations, two in California and two in the Hawaiian Islands. Additional low frequency transmission observations from the permanent sound channel at mid-depths will not be available until these installations have been completed.

Under Dr. Hersey's direction "Atlantis" has undertaken a systematic program of measuring the acoustical reflectivity of the bottom in deep water. Such measurements can be obtained at each hydrographic station without delaying the progress of the cruise. A most interesting development is that at many of the stations reflections have been obtained from considerable distances below the bottom. Thus it seems possible that through further studies of the velocity of sound in bottom deposits and through some additional refinements in instrumentation it may soon become possible to map stratification in the sedimentary material which has been so long accumulating. Dr. Ewing is much interested in this phase of the program.

Another acoustical development of great biological interest is that systematic observations on the depth of the so-called scattering layer, obtained through the new recording sonic sounder on "Atlantis", are beginning to show that the diurnal migration of this layer occurs with great regularity and consistency. Everywhere "Atlantis" has cruised during recent months the layer has been located, by day at about 300 fathoms and by night at about 50 fathoms. It is clear that we are here dealing with the vertical migration of plankton organisms, perhaps mainly euphausids, but whether the backward scattering of sound, which in some instances is at least as strong as the echo from the bottom, comes from such small animals or from the fish which may be feeding on them, has yet to be shown. Sonic echoes from schools of fish have, of course, frequently been observed in shallow water. If the scattering layer in the deep ocean is also due to fish, our estimates of the total population will have to be greatly revised.

11. Underwater Explosive Phenomena.

The work of the Underwater Explosive Research Laboratory, directed by Dr. Paul M. Fye, continued under contract with the Bureau of Ordnance, Navy Department, throughout the year. Although originally the group working at Woods Hole on explosive phenomena had been thought of as a laboratory within a laboratory, this distinction has gradually almost completely disappeared. Not only have explosives become an important tool in oceanography, but also the specialist in underwater explosive phenomena has found that the environment plays an important part in the success of his experiments. However, it has become clear that there are too many people living in and near Woods Hole to make it practical to continue experimentation with explosives in local waters in peacetime. Thus the present plan is to terminate this project during the next year. Many of the results of this work are beginning to appear in the appropriate physical journals.

V. STAFF

(As of December 31, 1946)

Columbus O'D. Iselin, Associate Professor of Physical Oceanography, Harvard University, and Associate Curator of Oceanography, Museum of Comparative Zoology; Director.

Alfred C. Redfield, Professor of Physiology, Harvard University; Associate Director and Senior Biologist.

John C. Ayers, Research Associate in Biology.

Dean F. Bumpus, Associate in Oceanography.

Andrew F. Bunker, Research Associate in Meteorology.

Cornelia L. Carey, Associate Professor of Botany, Barnard College; Associate in Marine Bacteriology.

George L. Clarke, Associate Professor of Zoology, Harvard University; Marine Biologist.

William Maurice Ewing, Associate Professor of Geology, Columbia University; Associate in Geophysics.

Charles J. Fish, Consultant on Marine Biology, Rhode Island State College; Marine Biologist.

William L. Ford, Research Associate in Chemical Oceanography.

Frederick C. Fuglister, Research Associate in Physical Oceanography.

Paul M. Fye, Associate in Chemistry.

John B. Hersey, Research Associate in Underwater Acoustics.

Louis W. Hutchins, Marine Biologist.

Bostwick H. Ketchum, Marine Bacteriologist.

Arthur Klebba, Research Associate in Physics.

Raymond B. Montgomery, Physical Oceanographer.

Fred B Phleger, Jr., Associate Professor of Geology, Amherst College; Associate in Submarine Geology.

Martin J. Pollak, Research Associate in Physical Oceanography.

Charles E. Renn, Department of Sanitary Engineering, Johns Hopkins University; Associate in Marine Bacteriology.

Gordon A. Riley, Assistant Professor, Bingham Oceanographic Laboratory; Marine Physiologist.

C. G. Rossby, Professor of Meteorology, University of Chicago; Associate in Physical Oceanography.

Wyman C. Rutledge, Research Associate in Physics.

Mary Sears, Planktonologist.

H. R. Seiwell, Physical Oceanographer.

Floyd M. Soule, Commander, U. S. Coast Guard Reserve; Associate in Physical Oceanography.

Athelstan F. Spilhaus, Professor of Meteorology, New York University; Associate in Physical Oceanography.

Henry C. Stetson, Associate Curator of Oceanography and Alexander Agassiz Fellow, Museum of Comparative Zoology; Submarine Geologist.

Henry M. Stommel, Research Associate in Physical Oceanography.

Harry J. Turner, Research Associate in Marine Biology.

Allyn C. Vine, Physical Oceanographer.

William S. von Arx, Research Associate in Physical Oceanography.

Edmond E. Watson, Associate Professor of Physics, Queen's University; Associate in Physical Oceanography.

Charles M. Weiss, Research Associate in Bacteriology.

Alfred H. Woodcock, Physical Oceanographer.

George P. Woollard, Physical Oceanographer.

J. Lamar Worzel, Research Associate in Geophysics.

Jeffries Wyman, Associate Professor of Biology, Harvard University; Associate in Oceanography.

John McGilvray, Comptroller.

Helen F. Phillips, Secretary to the Director.

William C. Schroeder, Business Manager.

William Schroeder, Superintendent of Buildings and Grounds.

List of Contributions

LIST OF CONTRIBUTIONS

FROM THE WOODS HOLE OCEANOGRAPHIC INSTITUTION

For a list of Contribution Numbers 1 to 100 see previous issues from 1933 to 1940. A separate list of these numbers may be obtained on request.

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